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HEAD CHARACTERS OF THE ODONATA

With Special Reference to the Development of the Compound Eye

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CONTENTS

I. INTRODUCTION

In the order Odonata the head characters are of great taxonomic value. Aside from mouthparts, they have been little studied. The aim of the present paper is to present facts concerning head structure that have been investigated and observed and to indicate their bearing on relationship within the order.

II. THE PRINCIPAL TYPES OF THE ODONATE HEAD

The form of the head in the Order Odonata exhibits great variations. The most obvious fact is the extraordinary development of the organs of sight. This development is accomplished either by enlarging the two compound eyes so as to increase the field and the number of the optical elements, as in the Anisoptera; or by pushing the compound eyes far apart, placing them on the lateral stalk-like ocular lobe so as to facilitate a wider range of vision, as is exhibited in the Zygoptera. The maximum development of both of these plans has been reached by the higher forms of the two suborders, and at the same time, the stages which lead up to these results are still preserved in the different lower forms. Thus we have the following principal types of head forms.

ANISOPTERA

The Gomphinae and the Petalurinae.—These lie nearest to the primitive type. The eyes are not excessively large and are wide apart; width of epicranium separating the eyes is less than the diameter of the eye. Occiput broad, forming an occipital shelf; vertex variable; ocelli arranged into an approximately straight transverse line; antennae four-segmented. Example: *Gomphus abdominalis,* Pls. VII; VIII, Fig. 1, and Pl. XV, Fig. 5.

The Cordulegasterinae.—The eyes become more or less approximated on the dorsal side but just fail to touch each other (some members of this sub-family have eyes just meeting at a point); occiput forming a shelf, subquadrate in shape; vertex flat but much reduced in width on account of the encroaching of the eyes; post and ante-clypeus well differentiated; ocelli are arranged in a nearly straight line; antennae seven-segmented. Example: *Anotogaster kuchenbeiseri,* Pls. VII; VIII, Fig. 2.

The Libellulinae.—The eyes become excessively large, encroaching upon the facial region, and thus affect the size and proportions of the facial sclerites; they meet on the mid-dorsal line for a considerable distance except in *Diastatops.* The front portion of the occiput is compressed into a thin sheet between the eyes, the posterior portion becomes a small occipital triangle; the vertex becomes a raised, constricted plateau with two lateral ocelli sticking out on its sides, its bulging front wall arches over the median ocellus; frons bulging, prominent; antennae six-segmented. Example: *Pantala flavescens,* Pls. VII; VIII, Fig. 3.

The Aeschninae.—The enlargement of the eyes reaches its maximum development. The eyes become enormous, and confluent with each other along the mid-dorsal line for a great distance; vertex reduced to a very small raised hump, occipital triangle very small; lateral ocelli are not in straight line with the median ocellus; antennae seven-segmented. Example: *Anax parthenope,* Pls. VII; VIII, Fig. 5, and Pl. XV, Fig. 4.

The Epiophlebiidae.—This is probably a side branch of this development. The eyes are enlarged to a great size, approaching each other but failing to touch; occiput becomes reduced to a small sub-circular shelf; vertex is excessively developed, forming a prominent shelf-like structure, projecting far out from the forehead region; the arrangement of the ocelli is most remarkably modified by the abnormal development of the vertex, the lateral ocelli migrate backward and are located at the caudal margin of the vertex being not visible from the front; antennae 5-segmented. Example: *Epiophlebia superstes,* Pls. VII; VIII, Fig. 6.

ZYGOPTERA

The Agrioninae.—The head characters show the most generalized condition in this Suborder. The eyes are separated by a width of epicranium greater than the diameter of a single eye; the post ocular lobe is not well developed, its diameter never exceeds that of the eye; post ocular suture poorly developed; epicranial suture absent; antennae located nearer to the epistomal suture, clavola not segmented, its length always similar to that of the scape and pedicel. Example: *Agrion atratum,* Pls. VII; VIII, Fig. 7.

The Lestinae.—This shows a step of advancement in development, the post ocular lobe is better developed, the dorsal half of the eye is pushed outward, and the inner eye margins are not parallel with each other; clavola of antennae segmented. Epicranial suture present. Example: *Lestes forcipatus,* Pls. VII; VIII, Fig. 8.

The Coenagrioninae.—The higher forms of this sub-family show maximum of head widening. The development of the post ocular lobe is accompanied by a development of the post-genal region; the epicranium becomes transversely elongated forming a kind of cross-stalk carrying the two eyes at its ends; epicranial suture present; antennae located further from the epistomal suture, clavola not segmented, its length greater than that of the scape and pedicel together. Example: *Platycnemis annulata,* Pl. VII, Fig. 9.

III. THE ENDOSKELETON

The head of the dragonflies is a specialized structure. The compound eyes have grown to enormous size occupying the greater part of the surface. In order to accommodate these huge visual organs the exoskeleton (facial sclerites) has undergone profound modifications. The endoskeleton (tentorium) though modified and much elaborated, agrees in its construction with the typical arrangement which is characteristic of all the Pterygote insects.

The tentorium consists fundamentally of three pairs of tentorial arms (anterior, dorsal and posterior arms) which originate as hollow invaginations of the head wall. These invaginations grow deep into the head cavity until they meet each other just in front of the occipital foramen and fuse across the median line to form a central tentorial body; this is shaped like a transverse bar, appearing as the floor of the foramen.

The anterior and dorsal pairs of the arms are typical. Modifications of the tentorium occurs however in the occipital region. In most of the generalized insects the tentorial pits are plainly to be seen and serve for the identification of the origin of the tentorial invaginations. In the dragonflies the posterior arms are so short and broad and the tentorial pits are so completely fused and atrophied that their presence is almost unrecognizable (Pl. X, Fig. 6). This is true of the adult. But in the nymph stage they are not yet modified and are easily identified.

This modification in the adult stage is evidently brought about by the abnormal development of the nymphal labium. In order to show the nature of this modification and its relationship with the development of the labium, a description of the endoskeleton of the nymphal head is necessary.

A. The Nymphal Tentorium

The tentorium of the nymphal head is generalized. The posterior arms lying on the lower ends of the occipital formamen, though short and broad, are recognizable. The tentorial pits (Pl. IX, Fig. 4, pt) are distinct and wide, leaving no doubt as to the identity of these invaginations.

The anterior arms (Pl. IX, Figs. 2, 4, AT) are long and strong, and slightly twisted toward their roots which, when visible, appear as a pair of external pits lying between the gena and the trochantin just above the anterior articulation of the mandible (Pl. IX, Figs. 2, 4 at). On their ventral side there is a pair of mandibular processes (Pl. IX, Fig. 2, mdp) ; these are delicate tendinous structures, their distal ends expanded into round flaps buried in the muscles in the body of the mandible. Their function is probably merely that of anchoring the big jaws in place; the movement of the jaw is performed by other bundles of abductor and adductor muscles (Pl. IX, Figs. 2, 4, Ad. Md., Ab. Md.).

The dorsal tentorial arms appear as a pair of dorsal off-shoots of the anterior arms (Pl. IX, Fig. 4, DT). This is probably because these two pairs of tentorial invaginations fuse before they make contact with the posterior elements. The outer ends of the dorsal arms do not appear as true invaginations but are tendinous flaps attaching to the hypodermis of the facial wall near the base of the antennae. The points of attachment are indicated externally by slight elevations, one behind each antenna (Pl. IX, Fig. 1, DT).

The body of the tentorium is inconspicuous, extending transversely and appearing as the floor of the occipital foramen (Pl. IX, Figs. 2, 4, Tnt). In many cases there are on the ventral side of this central body two triangular projections (Pl. IX, Figs. 2, 3, VV), to whose surfaces two bundles of trunk muscles are attached. These projections are, however, not constant structures, since they are absent in the Libellulinae. In the Libellulinae the body of the tentorium is somewhat arched, and the maxillary abductor muscles are directly attached to its front border.

The Hypo-labial frame.—The endoskeleton of the nymphal head is complicated by the extraordinary development of the labium. The latter is highly specialized, serving the nymph as an unique raptorial organ. The mentum and the submentum are greatly enlarged and lengthened. The junction between them becomes a hinge, so that the labium, when at rest, can be folded together and directed backward, lying along the ventral surface of the body. The palpi are modified into movable lateral lobes, armed with elaborate hooks. (Pl. XIV and Pl. XVI). Movement of all the parts is controlled by muscles, tendons and ligaments, and during the action the whole organ can be thrown straight out with lightning-like rapidity. A powerful organ like this will naturally require some special device for its support. This requirement is fulfilled by an interesting modification of the hypopharynx.

The base of the submentum occupies an enormous space as shown in Plate IX, Figs. 3 and 5. This space, the labial cavity, is chiefly braced with an anchor-like structure. The long shank of this structure extends posteriorly from the hypopharynx and traverses the entire length of the labial cavity, dividing the latter into two lateral halves. The crown (Cwn) of this structure sits in a small pocket on the base of the submentum (Sml. pkt), while the two curved arms (Lat. a.) fit against the caudal rim of the cavity each terminating in a round fluke supporting the two latero-caudal corners. The antero-lateral rim of this cavity is framed by a pair of chitinous bars (HS). These, together with the anchor-like structure, form a complete framework, the sub-labial frame, supporting the whole circumference of the labial cavity and rendering it a strong base for the accommodation of the huge labium.

This anchor-like structure is obviously a modification of a hypopharyngeal apodeme. The mouth of the invagination (Pl. IX, Fig. 5, Mth) remains wide open like a pocket on the ventral side of the organ, the shank being merely a hollow tube. The chitinous bars on the antero-lateral corners of the labial cavity are the suspensorial plates of the hypopharynx found in common among the Pterygotes, but in this case very much enlarged. This sub-labial frame is found throughout this order of insects. In the Aeschnidae the labium is very long, the shank bearing at its middle portion a ventral projection, prominent and slightly curved downward and backward (Pl. IX, Figs. 5, 6, Vk). This is characteristic of this group and is not found in other Odonates.

The pair of triangular ventral projections on the body of the tentorium which has been mentioned above, when present, may also serve as a guide for the long shank of the sub-labial frame, because the shank, like the ventral nerve cord lies between them. The real relationship of these structures needs further investigation.

B. The Adult Tentorium

During the nymphal stage the submentum also covers the entire post-occipital region including the posterior tentorial arms and the lower half of the occipital foramen and consequently those parts that are covered remain membranous. During metamorphosis the big labium is cast off, and the original labial cavity is only in its lower half covered by the thin, plate-like adult labium (Pl. X, Fig. 6). The exposure of the upper half of this cavity brings about an extensive chitinization of the lower occipital region. The short and broad posterior tentorial arms are somewhat more expanded and become so heavily chitinized that their external pits become completely closed. In some species the mouths of the original pits can be detected as a pair of dark lines. This accounts, as has been already stated, for the obscurity of the typical tentorial arrangement of this caudal region.

In the Libellulinae there is a pair of occipital processes extending from the upper corner of the posterior arms, quite up to the upper margin of the sclerite (Pl. X, Fig. 3, ocp). Specimens treated with potash show that these processes are merely foldings of the occipital wall. This is probably a secondary development for strengthening the occiput, since it is present only in the Libellulinae, which are highly specialized forms in which the occiput attains the maximum size.

The true front border of the Odonate cranium is an internal epistomal ridge, lying between the anterior articulations of the mandible; with both ends in connection with the genae (Pl. X, Fig. 3, 5, er). This internal ridge is indicated externally by an epistomal suture, more commonly known as the fronto-clypeal suture since it is the dividing line of the frons and the clypeus. In dragonflies this epistomal suture is very prominent and deep, because the frons and clypeus are highly elevated (Pl. X, Fig. 4, er). The inturned edges of these sclerites along this suture fuse into a broad chitinous fronto-clypeal shelf (Pl. X, Figs. 4, 7, F. C. shf). The inner border of this shelf joins the internal epistomal ridge forming a strong bridge which braces the articulations of the jaws (Pl. X, Figs. 2, 3, 5, er). On both sides of this bridge, just beyond the mandibular articulations, are the external pits of the anterior tentorial arms. These are narrow slits lying between the genae and the trochantins. The latter are reflexible areas between the genae and the bases of the mandibles. The anterior tentorial arms, shaped like twisted flat tubes, extend from these pits inward and upward into the head cavity until they reach the caudal part of the cavity, where they join the body of tentorium (Pl. X, Figs. 4, 7, 8, At, Tnt). On the ventral surface of the anterior tentorial arms there are two pairs of processes. The anterior two of these are the mandibular processes (Pl. X, Figs. 4, 8, Mdp), they are delicate and tendinous, very similar to those of the nymphal tentorium; their round tips are inserted in the heavy muscles of the mandibles. The posterior pair are the maxillary processes (Pl. X, Figs. 4, 7, 8, Mxp), they are heavy projections arising from the inner end of the arm and with the maxillary abductor muscles attached to their anterior surfaces. These maxillary processes are not found in the nymphal head, but functionally they are homologous with the ventral triangular projections of the central body of the latter. The shifting of the maxillary muscles to this anterior position is probably due to the increase of the depth of the head through the metamorphosis.

The dorsal pair of the tentorial arms is always the simplest. They extend from the dorsal side of the inner ends of the anterior tentorial arms, straight to the bases of the antennae (Pl. X, Figs. 4, 7, 8, Dt). The most marked difference between the dorsal tentorial arms of the adult and those of the nymph is that in the latter the outer ends are merely tendinous flaps attached to the hypodermis of the facial wall, while, in the adult these ends are represented by a pair of tentorial pits (Pl. X, Fig. 1, Dt). These pits are not visible in natural condition but can be traced when treated with potash. In the Sub-order Zygoptera, especially the Agrionidae, these dorsal tentorial pits are very distinct.

Another pronounced change in head of the dragonflies during metamorphosis is the extraordinary development of the compound eyes. The disturbance caused by the extension of these enormous visual organs into the facial area and the subsequent readjustment and modifications of the facial sclerites, is very remarkable, and will be discussed in another section of this paper. It is interesting, however, to see how the endoskeleton is involved in this abnormal development. Figure 1 of plate X illustrates the construction of the orbit of the compound eyes. This construction brings into cooperation three sclerites: the greater part of the ring is formed by the occiput which extends from beside the constricted vertex, arches over and covers the entire caudal and lateral sides; the front side of the ring is formed by the reflexed lateral edge of the frons (Fr.); the ventral side is formed by the gena. In the more primitive forms such as the Gomphidae, the genae, while serving as a part of the orbit, at the same time are exposed as part of the face (Pl. VII, Fig. 1). In the highly specialized forms the genae are completely concealed by the big eyes (Pl. VII, Figs. 3, 5). They serve not only as a part of the orbit but also for the attachment of the frons, and so have eventually become a part of the endoskeleton. Since the anterior tentorial arms arise as invaginations on the genae, these structures are in direct continuation one with another. And since the epistomal ridge is also in direct connection with the genae, therefore the tentorium, epistomal ridge and the genae form together an endoskeletal frame (Pl. X, Figs. 2, 4, 5). The trochantin which is counted by some authors as an individual sclerite of the head is also in direct continuation with the anterior arm. It is probably only an extension of the external end of the arm.

IV. THE EXOSKELETON

A. The Facial Region in the Anisoptera

Representatives of eighteen genera of Anisoptera were measured as to the length of each of the six facial sclerites, occiput, vertex, frons, postclypeus, anteclypeus, and labium, and the results are in part presented in the following table: The measurements were made with a micrometer eyepiece and reduced to comparable units.

The systematic range of the species measured is as follows: Numbers 1 to 8 of the following table are Aeschnidae, the first four being Aeschninae (*Gynancantha subinterrupta, Anax parthenope, Aeschnophlebia longistigma, Nasiaeschna pentacantha*), the fifth, Cordulegasterinae (*Anotogaster kuchenbeiseri*), and the sixth, seventh and eighth, Gomphinae (*Progomphus obscurus, Octogomphus specularis, Hagenius brevistylus*).

The last nine are Libellulidae, the first three being Cordulinae (*Epitheca marginata, Epicordulia princeps, Tetragonuria cynosura*), the next a Macrominae (*Epophthalmia elegans*), with the last five Libellulinae (*Pantala flavescens, Tramea chinensis, Crocothemis servilia, Acisoma panorpoides, Pseudothemis zonata*).

The last one is the rare and interesting sole representative of its family Epiophlebiidae: *Epiophlebia superstes.*

Topographical Measurements of the Facial Regions of Odonata–Anisoptera

No.	Occiput		Eyes		Frons		Clypeus		
	W.	L.	C.	D.	Post	Ante	Post	Ante	Labr.
1	2.6	3.0	10.0	0.0	7.0	6.0	7.0	2.6	5.0
2	2.5	2.0	10.0	0.0	10.0	6.0	10.0	3.0	5.0
3	6.5	4.5	8.0	0.0	8.0	5.0	10.0	3.7	6.5
4	5.0	4.0	6.0	0.0	10.0	4.0	8.0	3.0	5.0
5	10.0	6.0	0.0	7.0	8.0	4.6	4.0	5.0	8.0
6	10.0	4.0	0.0	5.0	4.5	3.0	3.0	4.5	6.7
7	10.0	2.7	0.0	7.3	6.5	3.3	2.3	2.3	4.5
8	10.0	4.5	0.0	5.0	6.0	5.0	3.3	3.5	4.5
9	10.0	6.5	2.5	0.0	9.0	5.0	5.0	2.5	5.0
10	10.0	5.5	5.6	0.0	10.0	5.0	6.7	7.5	5.7
11	10.0	8.3	5.0	0.0	8.3	10.0	1.5	5.6	6.6
12	6.0	6.0	2.0	0.0	10.0	6.0	9.0	0.6	8.0
13	10.0	8.5	6.5	0.0	6.6	6.0	6.6	3.8	3.8
14	9.0	9.0	3.6	0.0	10.0	5.0	10.0	1.3	5.0
15	8.3	8.3	3.4	0.0	8.5	9.0	10.0	1.6	6.6
16	8.0	6.3	0.8	0.0	8.0	10.0	4.0	2.0	6.0
17	8.3	10.0	1.6	0.0	0.0	0.0	4.0	2.5	5.6
18	6.7	3.5	0.0	6.7	8.5	10.0	5.0	3.5	6.7

In the preceding table the longest measurement is represented by the numeral 10 and the others by proportionate measurements. Column headings in this table indicate for the occiput, W—width, L—length; for the eyes, C—length of the suture when conjoined, and D—distance between eyes when separate; for the frons and clypeus, Post—the superior, and Ante—the anterior measurement on midline, and for the labrum, length.

In all these Anisoptera the head is wider than long, the excess in width ranging from one-eighth greater in *Aeschnophlebia* to one-half greater in *Anotogaster*. The vertex was so varied in form as hardly to admit of comparable measurements. It is smallest in the Aeschninae and largest (10) in *Epiophlebia*.

B. The Facial Region in the Zygoptera

In the head of the Anisoptera sutures separating occiput from vertex and vertex from frons are present, the sclerites although greatly modified in size and shape are yet recognizable. In the Zygoptera the above mentioned sutures are absent. Because of this it is difficult to determine homologies of the sclerites. In the Coenagrionidae an additional suture is secondarily developed as a result of the excessive enlargement of the postocular lobe. This suture, described more fully in the latter chapter, is designated by the writer as the postocular suture (Pl. VII, Fig. 8). Garman[1] called this suture the epicranial suture. If his supposition is correct then the frontal region would include the antennae and all three ocelli which is contrary to the more commonly accepted belief that the antennae are never included in the frons. Snodgrass in his recent work on the head of insects[2] says " . . . The muscles of the labrum, some of the dilator muscles of the pharynx, and the retractors of the mouth angles, when present, have their origin on the frons. By these characters, especially the position of the median ocellus and the origin of the labral muscles, the true frontal region is to be identified when the frontal suture is imperfect or obsolete."

Fortunately the majority of the Coenagrioninae have both this postocular suture and the epicranial suture well preserved, leaving no doubt as to the identity of the frons. In this study the posterior

[1] Garman, P. The Zygoptera or Damselflies of Illinois. Bul. Ill. Sta. Lab. of Nat. Hist. 1917. 12. p. 423–424. pl. LX.

[2] Snodgrass, R. E. Morphology and evolution of the insect head and its appendages, Smithsonian Miscellaneous Collections. Vol. 81. p. 121–122.

edge of the median ocellus has been used as the caudal boundary of the frons when the epicranial suture is not present, and the measurements were taken from this point.

Measurements were made also of the head topography of thirty-nine genera of Zygoptera of which the systematic range was as follows: In the thirteen Agrionidae used were representatives of seven Agrioninae and six Epallaginae. In the twenty-six genera of Coenagrionidae, two were Megapodagrioninae, five were Lestinae, and nineteen were Coenagrioninae. The measurements taken were width and length of head and of occiput, diameter of the eye, length of vertex, of frons, of postclypeus, of anteclypeus, and of labrum. There is space here for only the means of the measurements taken and these are again expressed in terms of 10, this numeral always representing the width of the head which is the longest of these measurements. The others are in proportion.

Comparison of the Means of Measurements of the Head of the Five Subfamilies of Zygoptera

	Head : W. : L.		Occiput : W. : L.		D. of E.	L. of V.	L. of F.	L. of Pc.	L. of Ac.	L. of Lr.
Agrioninae	10	5.1	2.5	.20	4.6	1.3	1.7	0.8	0.8	1.0
Epallaginae	10	4.9	2.2	.20	4.4	1.1	1.9	0.9	0.8	1.0
Megapod'nae	10	5.1	2.4	.40	4.4	1.0	1.9	0.9	0.7	1.1
Lestinae	10	4.9	2.3	.20	4.8	1.0	1.8	0.8	0.9	1.1
Coenagr'nae	10	4.4	2.1	.19	4.9	0.9	1.9	0.8	0.7	1.1

In striking contrast with the Anisoptera, where the enormous enlargement of the compound eyes greatly affects the size and proportions of the facial sclerites, the Zygoptera are remarkably uniform.

A few of the head characters of the Zygoptera are of considerable taxonomic value. These characters are, briefly, as follows:

a. The epicranial suture, when present, begins near the caudal margin of the dorsum, extends forward between the lateral ocelli and forks just behind the median ocellus. The branches extend only for a short distance, rarely beyond the base of the antennae as is best shown in the *Lestes* (Pl. VII, Fig. 8). This suture is present in every Coenagrionine but is absent in the Agrioninae—*Hetaerina* being the exception of the latter group.

b. **The postocellar suture**, in its median portion, when well developed is closely parallel to the hind margin of the dorsum. Its ends extend latero-anteriorly behind the ocelli to the inner margin of the compound eyes. In the Coenagrionidae this suture is distinct and serves as a dividing line, separating the postocular lobe from the facial regions (Pl. VII, Fig. 8). In the Agrionidae however this suture is not well developed, being represented only by a pair of short transverse grooves running mesally from the inner margins of the compound eyes (Pl. VII, Fig. 7).

c. **The antennae** are always located below the level of the frontal suture (Pl. VII, Fig. 7) in the Agrionidae, while in the Coenagrioninae the location of the antennae is always above or on the same level with the frontal furrow (Pl. VII, Figs. 8, 9).

d. **The postocular lobe** is always more developed in the Coenagrionidae than in the Agrionidae. In the former its diameter often exceeds that of the compound eye.

e. The number and relative length of the segments of the antennae. This will be discussed in the next section.

V. THE ODONATE ANTENNA

The antennae of this order are all short and inconspicuous. They are all setaceous, but vary considerably in shape and in number of segments. The basal two segments (scape and pedicel) are much thicker; the clavola or flagellum is slender and bristle-like, consisting of from one to five segments.

The antennae of the Gomphines are of four segments (Pl. XI, Figs. 1, 11). The last segment is the longest and is much longer than the others. The scape and pedicel are usually similar in length.

With the exception of a few primitive forms, the antennae of the Aeschnines are of seven segments. The third segment is the longest, the fourth is the shortest, especially in *Anaciaeschna* (Pl. XI, Fig. 3). The antennae of *Gomphaeschna* have only five segments and the third is the longest (Pl. XI, Fig. 8). The antennae of the *Caliaeschna* has only six segments (Pl. XI, Fig. 10), the second segment being the longest.

The Cordulegasterinae, also, have seven-segmented antennae. The pedicel is the longest segment (Pl. XI, Fig. 2). The third segment comes next in length, and the scape is short, being only half as long as the pedicel. The distal four segments are similar in length.

The Cordulines and Macromiines are very similar, the antennae being composed of six segments; (Pl. XI, Fig. 4). The third is longest. The other segments, including the scape and pedicel, are uniform in length.

All the Libellulines have six-segmented antennae, and the majority have the last segment longest. The third segment is longest in *Potamarcha, Pantala, Tramea,* and *Trithemis.* In *Sympetrum* the third and sixth are nearly equal in length.

In the isolated and very peculiar *Epiophlebia* the five-segmented antennae have the second joint nearly twice as long as the third, broadly dilated and hairy on the lateral margins.

In the Sub-order Zygoptera, with the Lestines as the only exception, the clavola is not segmented, and the number of the segments in the antennae, therefore, is three.

In the Agrioninae the clavola is the longest segment. The scape and pedicel are similar in length and are always longer than half the length of the clavola. *Hetaerina* is an exception in that the scape is slightly longest (Pl. XI, Fig. 17).

In Coenagrioninae the clavola is longest but the scape is noticeably longer than the pedicel (Pl. XI, Fig. 14) and it is always shorter than half the length of the clavola.

In the Epallaginae the clavola is also the longest; the two basal segments are not constant in length, their characters fluctuating between those of the Agrioninae and Coenagrioninae.

In the Lestinae the clavola is two-segmented (Pl. XI, Fig. 3). In several cases three segments are observable, but in that case the distal two segments are never well differentiated. The segmented condition of the clavola is best shown in *Sinolestes* (Pl. XI, Fig. 21).

The form of the adult antennae is not correlated with that of the nymphal stages, especially when the length of the segments is concerned. In the nymph of Agrionines the scape is hypertrophied; its length exceeds that of all the remaining segments put together; while in the adult stage it is the unsegmented clavola that is longest (Pl. XI, Figs. H and 18). Another good example is *Hagenius.* In the nymph of this species the third segment is flattened and very broad (Pl. XI, Fig. B), while in the adult this segment is the shortest and the fourth segment very long.

The segments of the clavola of the insect are never provided with muscles. This suggests that the sub-segmentation of the clavola is a secondary character. The fully developed Odonate nymphs with the exception of the burrowing forms—Gomphines,

PROPORTIONATE LENGTH OF ANTENNAL SEGMENTS IN ADULT ANISOPTERA

	Segments						
	1	2	3	4	5	6	7
Progomphus obscurus	2	2	1.5	10			
Octogomphus specularis	3	3	2	10			
Ictinus pertinax	3.5	3.5	3	10			
Gomphidia confluens	2	3.5	2	10			
Anisogomphus flavescens	2	2	1	10			
Gomphus abdominalis	2	2.5	1.5	10			
Lanthus albistylus	2.5	2.5	2	10			
Zonophora batesi	1.5	1.5	1	10			
Gomphaeschna furcillata	7	8	10	6	5		
Caliaeschna sp.?	4	10	6	3	3		
Basiaeschna janata	5.5	8.9	10	6	6.7	5.5	4.5
Aeschna umbrosa	5	5	10	5	6	5	5
Anax junius	5	6	10	4	6	6	5
Planaeschna	4	7	10	4	5.5	5.5	4
Gynancantha subinterrupta	5	6.5	10	4	5	6	5
Anaciaeschna jaspidea	4	6	10	1.5	3	3.5	8
Chlorogomphus papilio	4	10	4	2.5	2.5	2	2
Anotogastes kuchenbeiseri	5	10	9	4	5	5	4
Cordulegastes diastatops	5	10	7	3	3	3	4
Epiophlebia superstes	4	10	6	3	3		
Epophthalmia elegans	6	6	10	5	5	6	
Epitheca marginata	6	7	10	7	8	8	
Tetragonuria cynosura	6.7	7.5	10	7.5	8	8.5	
Didymops transversa	7	7	10	6.5	8	9	
Nannophya pygmaea	3	6	5	2	4	10	
Diplacodes trivialis	4	7	8	6	7	10	
Neurothemis tullia	4	6	7.5	5	7.5	10	
Deielia phaon	5	7	7	4	7	10	
Brachythemis contaminata	4	6	6	3.5	6	10	
Crocothemis servilia	3	7	8	4	6	10	
Celithemis amanda	5	7.5	10	7.5	7.5	9	
Rhyothemis fuliginosa	6	7	8	5	6	10	
Palpopleura sexmaculata	3	6	6	3.5	4	10	
Libellula angelina	4	7	8	5	6	10	
Othetrum albistylum	6	7	9	5	6	10	
Lyriothemis pachygastra	5	7	8	5	5	10	
Pseudothemis zonata	3	5	8	5	5	10	
Brachydiplax chalebea	4	6	7	6	7	10	
Sympetrum baccha	4	7	10	6	7	9.8	
Plathemis lydia	4	6	10	7	7	10	
Acisoma panorpoides	4	6	7	4	6	10	
Tramea chinensis	3	3.5	10	6	8	10	
Pantala flavescens	3	7	10	5	6	7	
Hydrobasileus croceus	4	5	9	6.5	9	10	
Tholymis citrina	5	5	8.5	5	7	10	

which have four (Pl. XI, Figs. B and C), and Petalurines, which have six segments (Pl. XI, Fig. 1)—all have seven-segmented antennae (Pl. XI, Figs. D, E, F, G, H). The reduction of the number and size of segments of the adult antennae is therefore a matter of degeneration. The degeneration of this organ is no doubt correlated with the extraordinary increase of visual power, which is one of the most prominent characteristics of the order.

The data on which the preceding generalizations are based is in the preceding table. The longest segment is set down as 10; the others in proportion.

VI. DEVELOPMENT OF THE COMPOUND EYES

A. Development During the Nymphal Stage

The external features of the nymphal head.—A few terms applied to the larval head need to be defined, since they will be mentioned frequently in the following discussion. A full description of the general structure of the larval head is not necessary.

The dorsal aspect of *Aeschna* larvae of young, mature and intermediate stages are shown in Plates XII and XIII, Fig. 1. During the early instars the sutures of the upper facial region are not distinct, the epicranial sclerites can only be referred to according to their respective regions. In an older larva the positions of the ocelli which usually indicate the boundary of the vertex became clearly marked on the cuticle. Thereafter the sclerites of the epicranial region can be more definitely distinguished. The figures show that the eyes are antero-laterally placed. The occiput is conspicuous, and expands laterally into two prominent postocular lobes. The coronal or epicranial suture (Epi.S) is very distinct. It extends from the occipital foramen to the anterior border of the occiput where it forks abruptly; each arm turns at a right angle and extends laterally outward until it meets the caudal angle of the eye. In later development the caudal angles of the eyes grow like wedges and invade the occipital region along these sutures. The vertex is marked off posteriorly by the arms of the coronal suture, anteriorly and laterally by the developing ocelli. In *Gynacantha* this sclerite is almost a perfect square. The frons is bounded posteriorly by the median ocellus and anteriorly by the epistomal (fronto-clypeal) suture which is always very distinct. On each side of the frons is the base of an antenna; instead of being a typical ring-like antennal sclerite it appears like an extra segment of the antenna. The antennae are much more prominent than in imago. The clypeus and labrum are well formed. Lateral and closely adjacent to the base of each antenna is an ovate cuticlar elevation, this is the external sign of the attachment of the dorsal tentorial arm (Dt). Immediately lateral to this tentorial elevation, and extending all the way along the inner border of the eye is a long and wide crest-like structure; the cuticle of this whole region is tough and much wrinkled (B.Z.) This structure is of great importance in the development of the compound eye. The thick cuticle serves as a roof covering the underlying tissue which, as later experiments confirm, consists entirely of young buds of future ommatidia. This special feature is designated under the name "Budding-zone."

The most striking character of the Odonate larval head is the labium. It is highly specialized, and unique in the animal kingdom. Its structure and function have been described in the section dealing with the larval tentorium. A lateral view of the head of an Aeschnine larva (Plate XIV, Fig. 3), shows that the labium in the Aeschninae is greatly elongated. The distal half is flat and straight, and when at rest the whole organ is folded and concealed under the head. The head is also dorso-ventrally flattened; it appears as if the two were so modified to accommodate each other.

In Libellulidae the labium is more elaborate. The median lobe is projecting and triangular; the lateral lobes, formed by the original labial palpi, are huge, triangular and very concave. They meet together along their distal borders above the median lobe. The whole organ is spoon-shaped (Plate XIV, Fig. 1, and Plate XVI, Fig. 4), and covers the lower half of the face like a mask. The head is more or less spherical.

In a flat head like that of the Aeschinae, the front surface is greatly reduced and the eyes tend to spread out more or less in a single plane. But, when a head is sub-spherical, as in the Libellinae, it offers a great space on the front side for the development of the eyes. Another point of difference is that in the Libelluline larval head the cuticle covering the budding-zone does not form a shelf-like structure as in the Aeschnine larva; however, its location and boundaries can be clearly made out.

Experiments on the nymphs of Aeschninae.—The materials used for this experiment were young larvae of *Aeschna umbrosa.* Definite spots on the eye region of the young larval head were chosen and pricked with a fine needle to make slight wounds. The larva was then fed and its activities closely observed. Soon after the ecdysis, a careful examination was made of the growing head to trace the scars of the wounds, and the locations of these scars were then compared with those retained by the exuvium. Drawings were made to record the results. The same process was repeated on the same individual for a number of successive instars. The new prickings were made, each time, at least several hours after the molting in order to permit the expansion of the head which follows ecdysis.

The experiment was started on a very young larva with a head-width of 3.5 mm. Two punctures were made with a fine insect pin on the right eye region (Pl. XII, Fig. 1, scars Nos. 1, 2). Wound No. 1 was made on the root of the dorsal tentorial arm close to the base of the antenna: No. 2 was made on the middle of the budding-zone at the same level as No. 1. Since the head was so small the two punctures appeared very close to each other.

Having been wounded the larva dashed around in the water, then dived to the depths of the aquarium and attached itself to the under side of a stick with its head invariably pointing towards the bottom. Hiding from the strong light it remained motionless for a considerable length of time, but finally recovered from the excitement and began to feed voraciously.

The larva molted on August 17th, the size of the head was increased. The wounds caused by the prickings were carried by the growing head, partly concealed under the new cuticle and yet distinctly visible. The location of No. 1 remained unchanged because the wound fell upon tissues outside of the growing eye (Pl. XII, Fig. 1). The position of No. 2 moved laterally and came to lie on the outer edge of the budding-zone (Plate XII, Fig. 2).

Another remarkable fact following the molting was the appearance of a band of new tissue along the inner margin of the eye (Pl. XII, Fig. 2, N.T.). It was pale and contrasted plainly with the remaining parts of the eye which were more and less pigmented. The cuticle covering this band of new area was composed of small, compact and not well shaped facets, this structure being visible only with careful adjustment of focus under the binocular.

The scars of the wounds on the exuvium were very distinct; they were not new holes but were healed up, thickened and dark brownish in color. They remained in the same places where they were first made. Since the larva was still very young no additional wounds were made at this time. Towards the end of the instar it was observed that the new tissue became much darker in color, especially along the extreme boundary of the budding-zone where dark pigment granules were heavily distributed among the growing cells.

The larva molted again on August 31 (head-width of exuvium 4.5 mm.). Again a band of new tissue appeared on the inner margin of the eye (Pl. XII, Fig. 3, N.T.). Scar No. 1 sank deeper under the cuticle, still remaining on the same spot. Scar No. 2 now moved to the outside of the budding-zone; being pushed out by the new tissue. The scars became less distinct and were covered by new cuticle which bore almost no trace of damage (Pl. XII, Fig. 3, 2).

Since the larva had grown bigger it was then possible to experiment on both eyes. Two additional punctures were made, therefore, on the left eye (Pl. XII, Fig. 3, 3, 4) : No. 3 was made on the extreme outer edge of the budding-zone (a position comparable to No. 2 in Fig. 2). No. 4 was made on the dividing line between the pigmented and unpigmented tissue (a position exactly corresponding to No. 2 on the right eye). This puncture was made as a duplicate of No. 2 because the ommatidia covered by No. 2, although damaged, became more normal after each successive instar; their expansion caused the scar to become diffuse.

The next molting took place in September 14th (head-width of exuvium 4.9 mm.). Again a band of new tissue appeared on the inner margin of the eye, its caudal end showing slight differentiation (Pl. XII, Fig. 4, N.T.). It was noticed that the length of the band of new tissue increases rapidly instar after instar especially on the posterior half, its extension gradually invading the occiput. Scar No. 1 now became deeply buried under thick chitin, its location still remaining unaltered. Scar No. 3 moved from the edge of the budding-zone and became lodged on the new boundary line between the new and older tissues exactly in the same way as had happened to No. 2 in the previous molting. Scar No. 4 moved laterally and appeared within the pigmented region of the eye (Pl. XII, Fig. 4, 1, 3, 4). Another additional puncture was made on the extreme outer margin of the budding-zone (Pl. XII, Fig. 4, 5).

The larva molted again on October 4th, the head was then a little more than 7 mm. in width (head-width of exuvium 6.6 mm.). The scars of the wounds moved laterally as before, only No. 1 remaining unaltered in position. Scar No. 5 was pushed out by another band of new pale tissue; No. 3 moved to the pigmented area; No. 4 moved further laterally and became surrounded by well-shaped facets (Pl. XII, Fig. 5, 1, 3, 4, 5).

The most striking thing appearing in this instar was in the band of new tissue. It became obviously differentiated into two parts. The anterior portion exhibited nothing different from those of the previous instar, but the posterior portion appeared to be wider and the cuticle covering this portion appeared to be more rough and less transparent (Pl. XII, Fig. 4, 5, Nt., X.). These characters became still more pronounced toward the end of the instar. Unfortunately the larva died during the late period of this instar.

A fully mature larval head of this same species is shown in Pl. XIII, Fig. 1. It illustrates the subsequent development of this differentiated caudal portion of new tissue at the end of the larval life. Further experiments have confirmed that this patch of tissue is destined to form the big facets of the adult eye.

I have reared several larvae of *Anax junius*, a common species of another closely allied genus. An examination of the successive exuviae of any one of these specimens showed very definitely that the tissue destined to form the big facets of the adult eye begins to appear and grows very rapidly during the last three instars (Pl. XV, Figs. 1, 2, 3, X.). This offers a very useful supplement to the part which I failed to carry through in the above experiment with *Aeschna*.

Besides the facts stated above I have also observed the development of a series of longitudinal dark bands across the larval eye. Toward the end of every instar, shortly before another strip of new tissue is added from the budding-zone, black pigment granules form thickly along the intermediate boundary between the eye and the budding-zone (Pl. XI, Fig. 5). After the molting these pigment granules, being pushed out by the new tissue, establish themselves in the eye as a longitudinal dark band marking the boundary of the next older tissue. It was interesting to notice that the wounds made on the extreme outer margin of the budding-zone were found to coincide with the dark bands. This showed quite definitely that the series of dark bands on the eye indicate successive increases of tissue. It would be an excellent means of estimating the age of the larva, by counting the number of instars that the animal has gone through, but for the fact that the bands arising in the first few instars are confusedly combined into one mass, and the exact number of its components is obscured.

Experiments and observations on nymphs of Libellulidae.—I applied the same experimental method to four species of Libelluline larvae (*Plathemis lydia, Libellula pulchella, Sympetrum vicinum,* and *Tramea lacerata*), and found that the manner of development of the compound eye in these more specialized groups agrees in principle with that of the Aeschninae. That is to say, that the eye grows by accession of new tissues which arise from the budding-zone and are added to the inner margin from instar to instar. The result obtained from an experiment on *Plathemis lydia* was especially satisfactory because the longitudinal dark bands which mark the successive increases of new tissue are unusually distinct and conspicuous. The scars of the punctures made on the extreme margin of the eye or of the budding-zone were pushed out laterally by the new tissue and were found to coincide precisely with the longitudinal dark bands.

However, there are a few points of difference in details. The subsequent development of the eye tissue in the Libellulidae is more complex, and exhibits some special features which do not occur in the Aeschninae. These points of difference may be briefly stated as follows:

1. As a rule in the Aeschninae the eye tissue when first emerged from the budding-zone is pale and compact, but it eventually becomes pigmented before another stripe of tissue is added. Probably several instars are required to develop functional ommatidia. The larval eye tissues, arising either in the early or in the later instars, all go through the same process of development. In other words, the tissue arising from the successive instars becomes pigmented and develops into ommatidia following an uninterrupted order—all except the patch of tissue on the mesocaudal corner of the eye. This differentiates itself from the remaining parts of the eye, being deprived of pigments and protected under rough and usually pigmented cuticle. This patch of tissue comes from the caudal portion of the tissue arising in the last three instars. *Therefore in the eye of a grown Aeschnine larva there are two sets of distinctly distinguishable tissues* (Pl. XIII, Fig. 1, and Pl. XV, Fig. 3, X and Y).

In the Libelluline larva the tissue arising during the early instars ripens promptly into functional ommatidia. They are densely pigmented and the cuticle covering them develops into regularly six-sided facets. They occupy the dorso-lateral angles of the head and form the definitely projecting eyes of the larva. The late instars give rise to a big patch of tissue the caudal portion of which becomes distinctly differentiated and covered up by roughly wrinkled cuticle just as occurs in the Aeschnine larva. The anterior portion of this late patch of tissue exhibits, however, remarkable differences from those of the preceding instars. It occupies a considerable area extending far forward into the lower facial region. The ommatidia instead of ripening remain rudimentary and unpigmented and the cuticle of this region never bears regular facets. Not until toward the end of the last instar when the larva is almost mature does this region become rapidly and densely pigmented; after this the last metamorphosis promptly takes place. *Therefore in the eye of a grown Libelluline larva there are altogether three sets of distinctly distinguishable tissues* (Pl. XVI, Fig. 4, X, Y, Z).

2. Usually there are two transverse dark bands which extend between the budding-zone and the older pigmented tissue bridging over the unpigmented area. These dark bands do not appear in the very young larva. They begin to appear when the larva is nearly half grown and become more and more conspicuous as the eye keeps growing. They may be one or two, or they may be totally absent (as in *Pantala*). When two are present the upper one always extends closely along the front margin of the patch of tissue which is covered by rough cuticle and its inner end terminates near the base of the dorsal tentorial arm. The lower one always extends approximately half way between the upper band and the front margin of the eye and has its inner end directed toward the base of the anterior tentorial arm. The significance of these bands is not yet clear.

The longitudinal bands in Libellulinae vary in the different genera. In *Plathemis* and *Libellula* each instar gives rise to a band and the process continues throughout the larval life (Pl. XVIII, Fig. 3). In *Sympetrum* and *Mesothemis* the bands are very distinct, but are present only in the pigmented functional area; the late instars do not give rise to any of these bands. In *Tramea* the pigment granules appear only in the early instars and since they are confused they do not appear as regular rows. In *Pantala* the functional eye area becomes so intensely pigmented that these bands are totally obscured. In *Acisoma* the bands are present in the pigmented area but every one of them is broken at its middle portion so they look as if they were arranged in two transverse rows. In the other genera which I have examined the bands are all present, and their number varies from six to nine (counting the early combined ones as a single band). In most cases they are confined within the pigmented functional area and in many cases they are so diffused that they can be detected only by close adjustment of focus under the binocular microscope.

B. Development of the Compound Eyes during the Metamorphosis

The actual process of metamorphosis begins many days before the time of emergence. The change though internal, is expressed in a number of external characters and also in an alteration of behavior of the nymph.

The imaginal hypodermis of the labium shrinks from the cuticle and gradually retreats to the base of the submentum leaving the elaborate labium an empty shell. For this reason the nymph refuses to feed and remains quietly clinging to its support. In the meantime the color of the body becomes considerably darker and the whole body appears swollen, particularly the thoracic region. Owing to the developing of the large wing muscles, the wing-pads stand up vertically from the abdomen. The compound eyes swell up and extend far beyond the original eye boundary. This expansion of the eyes is distinctly visible through the cuticle, especially in the occipital region where the two eyes approach or actually touch each other pushing the prominent occiput out of its original position (Pl. XVIII, Fig. 2, X, X, X). When these changes are in progress the thoracic spiracles become functional. The nymph protrudes its head and later its thorax from the water. It may remain clinging to its support in this manner for hours or even for several days before emergence.

The transformation which develops the adult eye from nymphal structure is a marvelous phenomenon of nature; a detailed description of which is beyond the scope of this paper. For the benefit of the present discussion the main characters of an adult eye will be here stated. In a typical adult eye of the dragonfly the ommatidia are differentiated into two groups. Those of the upper group have bigger cones, consequently the facets are larger. The pigmentation is usually absent. Those in the lower group have smaller facets and the pigmentation is very dense. In Libellulinae the two portions of the eye show different, or even strongly contrasting, colors. The big and small facets are marked off so sharply that eventually a transitional line appears between them. There is always a gradation between the two groups although the gradation varies greatly in degree among different forms. In some lower forms the change in size is so gradual that a transitional line is almost unrecognizable. The ommatidia on the margin of the eye, especially those on the lateral border where the eye is reflexed backwards, are usually not well formed. The facets of these regions are either deformed or indistinct and the pigmentation is very light or even totally absent. In short, these ommatidia are much less perfect as compared with those which are closer to the facial region.

Material used for this experiment were full grown or younger nymphs collected from different localities at Ithaca, N. Y. The experiments covered the following species:

Aeschna umbrosa	*Sympetrum vicinum*
Anax junius	*Tramea lacerata*
Gomphus lividus	*Plathemis lydia*
Tetragonuria cynosura	*Ischnura verticalis*
Libellula pulchella	

The experiments were made by the same pricking method. Definite spots on the nymphal eye region were chosen and pricked with fine needle to make slight wounds. After the metamorphosis, when the adult head was fully expanded, a careful examination was made of the adult eye to trace the marks of the wounds and the locations of these marks or scars were then compared with those retained by the exuvium. Since an individual nymph can tolerate only a few wounds without upsetting its normal development, experiments on each species were carried by a number of individuals. The results obtained from the different individuals are here recorded all together on only a few drawings.

I emphasized the fact that the actual expansion of the eye tissue takes place days before the emergence, therefore, in this experiment all of the punctures were made on the nymphal head before the animal became fully mature. Mature nymphs do not serve the purpose.

X, Y and *Z* Tissues.—In the preceding section I have stated that by the end of nymphal stage different sets of eye tissues are present in the nymphal eye region, and that they grow together like a piece of mosaic. In order to avoid unnecessary repetitions of wording I propose the following abbreviations:

X tissue.—For the tissue which in all cases occupies the posterior corner of the nymphal eye and is covered by wrinkled cuticle, being deprived of pigmentation.

Y tissue.—For the functional nymphal ommatidia which in all cases possess regular facets and are deeply pigmented.

Z tissue.—For the non-functional late-developing tissue of such nymphs as *Libellula.* They do not possess regular facets and remain rudimentary and unpigmented until the end of the nymphal stage.

1. **Experiments on Aeschna umbrosa.**—In the eye of a mature nymph of this species only X and Y tissues are present as has already been mentionad. Attention is called to the fact that the part of the Y tissue immediately bordering the budding-zone, although pigmented has never functioned during the nymphal stage. Apparently metamorphosis occurs before it ripens into functional ommatidia.

The dorsal aspect of the nymphal head is shown in Pl. XIII, Fig. 1. The dots record the locations of the punctures pricked on the heads of the different individuals used in this experiment. Figures 2 and 4 illustrate the dorsal and front views of an adult head of this species. Figure 3 is a lateral view of the adult head showing the left eye.

All the dots are labeled with Arabic numerals. All marks which correspond are labeled by the same number, no matter where they appear in these figures.

The record shows the following facts:

1. Scars of all punctures made on the X tissue of the nymphal head appear on the adult head within the area of the big ommatidia.

2. Scars of all punctures made on the Y tissue of the nymphal head appear on the lower lateral portion of the adult eye within the small area of the ommatidia.

3. Scars of all punctures made on the boundary line between the X and Y tissues of the nymphal head appear exactly or approximately coincident with the transitional line of the adult eye. The transitional line of the adult eye in this species is not very distinct, and is deeply curved.

4. Scars of all punctures made on the budding-zone of the nymphal head appear within the area of the small ommatidia of the adult eye, closer to the facial region.

5. Often in this species the longitudinal dark bands of the nymphal eye persist through the metamorphosis. Although only fairly recognizable they serve as excellent landmarks indicating the share which the Y tissue takes in the construction of the adult eye. In the nymphal eye these bands arrange themselves in longitudinal rows, parallel but slightly curved with their concave sides toward the facial region. After metamorphosis the orientation of these bands is altered; the ends of the bands bend away from the facial region.

6. Very often the ruptured cuticle when healing up forms a sharp scar pressing upon the underlying tissue. During the expansion of the eye the scar, being fixed and immovable, scratches the delicate unfolding tissue and thus causes an extended wound which appears later on the adult eye as a linear white scar, as is illustrated in Plate XIII, Figure 2, small, No. 18, and in Plate XVI, Figure 5, small, Nos. 3 and 18.

These facts confirm the following points:

1. The X tissue is destined to form the big ommatidia.

2. The Y tissue, or the functional nymphal eye, is retained as a part of the adult eye in this species. It is within the area of the small ommatidia, constituting the lower lateral portion of the eye —the part which flexed rearward.

3. The main portion of the small ommatidia of the adult eye arises from tissues occupying the budding-zone and the region immediately adjacent to the budding-zone.

4. Great expansion and distortion of tissues occur during the metamorphosis.

2. **Experiments on Anax junius.**—Plate XV, Figs. 3 and 4 record the results of experiments on *Anax junius.* In this species the X and Y tissues keep to a distinct boundary line. Punctures were made purposely to cover this dividing line. The results of these trials were very satisfactory. The record shows nothing noticeably different from that of the *Aeschna umbrosa* except that in this species the big and small ommatidia are better differentiated and consequently the transitional line is more distinct.

3. **Experiments on Gomphus lividus.**—The nymph of Gomphus burrows in the bottom mud and its body structures exhibit many adaptive characters related to this habit. The dorsal aspects of the nymphal head of *Gomphus lividus* are shown in Plate XV, Fig. 7. The antennae appear swollen and conspicuous but each one is reduced to four segments. The bases of the antennae are raised and very broad, occupying a considerable part of the front (B.A.). The tentorial projections are inconspicuous (D.T.). The budding-zone on each side is marked off by grooves and is broader at its posterior end (B.Z.). The facets of the eyes are very well developed in the young nymphs, but development seems subject to the law of use and disuse. In a full grown nymph the eye does not appear to be a very efficient organ; the cuticle is thick and opaque. The facets are exceedingly small in size, those on the side —the older tissues—are better formed but not comparable with those of the Libellulinae. The X tissue appears very late in the

nymphal stage, occupying a small area and is not sharply distinguishable from the remaining parts of the eye; superficially it can only be recognized by its slightly wrinkled cuticle.

The adult eye of *Gomphus* is not excessively large and the two eyes are separated by a wide occipital shelf (Pl. VII, Fig. 1, and Pl. VIII, Fig. 1). The big ommatidia are few in number and are irregularly grouped near the top of the eye. A great gradation of sizes occurs between the few regular big ommatidia and the regular small ones, the transitional line is therefore hardly recognizable.

Puncture No. 1 was made on the side among the better formed facets; No. 2 made on the extreme lateral border of the eye; Nos. 3 and 4 were made on the budding-zone and No. 5 made on the extreme inner margin of the eye (Pl. XV, Fig. 6, small, No. 5 and Fig. 7, small, Nos. 1, 2, 3, 4). The scars of these wounds appear on the adult eye in positions as are marked in Plate XV, Fig. 5, Nos. 1, 2, 3, 4, 5). They were affected by the expansion but the change is apparently not very great. No. 5 moved from the extreme lateral margin inwardly into the eye; this is quite contradictory to the results obtained from species of other groups.

The experiments on this species were done in the spring of 1931. At that time I did not notice the distinction of the different sets of tissues; furthermore, as has just been mentioned, the X tissue in this species is indistinct: therefore, no puncture was made to mark it. However, judging by the position of the scars of the other wounds, there can not be any doubt about the fact that the few irregularly grouped big ommatidia come from the poorly developed X tissue of the nymphal head.

4. **Experiments on Libellula pulchella.**—The head characters of the Libelluline nymph have been discussed in the previous sections. It is only necessary to repeat here that in the eye of a full grown nymph the three sets of tissues, X, Y, Z, are present.

The adult eye of the Libelluline is a wonder of nature. The big and small ommatidia contrast strikingly in sizes and colors. Most of the facets either big or small are regularly six-sided. The transitional line is extraordinarily distinct and is not so deeply curved.

The results of experiments on *Libellula pulchella* are shown in Plate XVI, Figs. 4, 5 and 6. This species is excellent material for this experiment not only because of its large size but also because the different sets of tissues of the eye are very distinctly differentiated. The X tissue is covered by coarse and darkly pigmented cuticle. The Y tissue forms the definite projecting nymphal eye. The Z tissue is broad and joins the X tissues end to end (Fig. 4, X, Y, Z).

These are the results obtained:

1. Scars of all punctures made on the X tissue appear on the adult head within the area of the large ommatidia.

2. Scars of all punctures made on the budding-zone and Z tissue appear on the area of the small facets which cover almost the entire lower portion of the adult eye.

3. Scars of all punctures made on the boundary line between the X and Y tissues appear quite accurately on the distinct transitional line of the adult eye.

4. Punctures No. 1 and No. 2, made near the center of the Y tissue, appear after metamorphosis on the extreme lateral margin of the adult eye (Fig. 6, scars 1 and 4), indicating that at least half of the nymphal eye has been pushed beyond the boundary of the adult eye.

5. Puncture No. 17 was made in contact with the tentorial elevation. This wound is not retained by the adult eye.

6. Punctures No. 7 and 7a were made close together on the margin of the budding-zone. After the metamorphosis the scars of these two wounds appear to be widely separated (Fig. 6, small numbers 7 and 7a).

7. A fold of membrane is found attaching on the lateral orbit just beyond the eye margin. When treated with KOH the membrane can be removed from the head and spread out like a pocket. It contains facets.

The differentiation of the Z tissue is common to nymphal heads which possess a spoon-shaped labium, but in the Libellulinae the growth of this tissue is particularly pronounced. In this experiment Z tissue gave rise to the majority of the small ommatidia. It seems to indicate that in the higher groups of the Anisoptera the development of the compound adult eye had achieved a more definite scheme. The nymphal eyes complete their growth a considerable length of time before the nymph is mature. The later nymphal life is spent in the development of sets of tissues which are definitely set off to serve the adult life. These late tissues are capable of great expansion, during the metamorphosis they unfold and build up the complete adult eye pushing the nymphal ommatidia quite to the lateral border where they are gradually discarded. The membrane-like fold found on the lateral orbit is the secondary cuticle of the nymphal eye formed during the last instar. It never gets a chance to develop fully but is pushed out as a fold and attaches itself behind the margin.

5. **Experiments on Tetragonuria cynosura.**—The nymphal eye of this Corduline nymph is small, rounded, and projects from the head prominently. The X and Z tissues are both present, they form a long but narrow patch bordering the inconspicuous budding-zone. The boundary line between the Y and Z tissues is not distinct. Plate XVI, Figs. 1, 2 and 3 record the experiment on *Tetragonuria cynosura.* The results agree with those recorded for Libellula except:

1. The large and small ommatidia are not so sharply marked off in sizes.

2. The transitional line is indistinct and is sharply curved.

3. The ommatidia of the nymphal eye are not absorbed wholly. The nymphal eye is folded backwards on the lateral border of the adult eye making a jog in the margin; this is the often-noted tubercle on the hind margin of the eye in the Cordulinae. Both facets and pigments are found on the tubercle.

6. **Experiments on Sympetrum and Tramea.**—The results of the experiments on these two showed no remarkable difference from those recorded for *Libellula.* The nymphal eye is first folded under the adult eye, projecting beyond the lateral border like a tubercle black with pigments, but as the imago matures it is gradually and completely absorbed. This is why in such specialized forms as *Sympetrum* and *Tramea* the lateral border of the adult eye appears to be straight and does not show any trace of the discarded nymphal eye.

The most noticeable difference between the eye features of a mature *Ischnura* nymph and those of the dragonfly nymphs is that in the former there is no external sign of differentiation of tissues. The whole eye is pigmented and its cuticle is thin and transparent. The X and Y tissues such as have been distinguished in the dragonflies do not appear in *Ischnura* nymphs.

Although great expansion of the visual tissue does occur during the metamorphosis, yet all the scars of the wounds I made in my experiments on the nymphal eye of this species appear on the adult eye in similar positions. This shows that the nymphal eye is completely retained by the adult, and that distortions and extensive shiftings of tissue do not occur during the transformation.

In the adult eye of this species, as well as other species of Zygoptera, the ommatidia are not sharply marked off into upper and lower halves by colors and sizes as in the dragonflies. All ommatidia are pigmented. Those close to the face are larger and are better formed, while those on the top, lateral and lower sides are comparatively smaller. The change is, however, very gradual, a transitional line like that of the dragonflies is not present.

Summary of Eye Development

1. The eye develops by receiving tissue from the budding-zone, added to the inner margin from instar to instar.

2. The new tissue consists of visual elements which are physiologically imperfect, and require further development to become functionally mature.

3. The late instars give rise to different sets of tissues, some of which may neither show any close affinity with those of the early instars nor exhibit any visual function during the larval stage.

Experiments trace the development of the compound eye during metamorphosis and confirm the destination of the different sets of tissues. The adult eye, especially in the higher forms of Anisoptera, comes from tissues which develop but never function during the nymphal stage.

4. The differentiation of the Z tissue from the Y tissue is most pronounced in the higher Libellulines in which it displaces the Y tissue completely. However, the Libellulidae are a large group, and there is variation among its members. The variation seems to be correlated with the form of the nymphal eye. Plate XVII illustrates roughly four principal types of variation. Figs. 1 and 1a are the front and dorsal aspects of the nymphal head of *Didymops transversa*—a Macromiine. The nymph buries itself in the bottom mud with the tips of the horn-like eyes projecting above the mud; well formed ommatidia are found only on the tips of the eyes. After metamorphosis the nymphal eye is pushed out by the Z tissue, folding backwards beyond the lateral border of the adult eye (Fig. 1b, NE) and is separated from it by a deep groove (g) which is in continuation with the contour of the lateral border of the eye.

In *Tetragonuria cynosura,* a Corduline, conditions are as shown in Pl. XVII, Figs. 2, 2a and 2b. The nymphal eye in this subfamily is small and projects from the head prominently. After metamorphosis, it is folded, as in Macromiine, backwards on the lateral border of the adult eye, making a jog on the margin but it is not separated from the adult eye by a groove (Fig. 2b, NE).

In both Macromiine and Corduline the vestigeal nymphal ommatidia are found within the pocket or the jog.

In the higher Libellulines the absorption of the nymphal ommatidia by the adult eye is complete, leaving no trace except the wrinkled membrane (Figs. 4, 4a and 4b).

The absorption, howerer, is a slow process; thus, in the newly emerged adult the discarded vestige is still apparent as a black projection beneath the membrane but it gradually disappears as the imago grows older.

In the ascending scale, from the lower to the higher forms, there is increasing modification. The improvement is made first by an enormous increase of area and number of the elements, as in *Cordulegaster;* then there is reduction in area and in the number of the elements but improvement in their size and uniformity. The development of the Y tissue is inversely proportional to the development of the X tissue.

The expansion of Z tissue after the metamorphosis in Libellulinae is very striking. It comes to occupy over half of the eye and expels almost the entire nymphal eye at the lateral border. So, the adult eye becomes a new and perfect organ by itself without the participation of the nymphal element.

VII. THE FACETS OF THE COMPOUND EYE

The facets are the corneal lenses of the ommatidia. They constitute the cuticular layer of the compound eye. I have been able to separate the cuticle of the eye of *Pantala flavescens* into six layers. In *Cordulegaster* I found many more, but was not able to find out the exact number. The thick cuticle of the Cordulegasterinae is probably due to the long last stadium the nymph undergoes.

The facets of the nymphal eye when fully formed are regular hexagons showing no difference from those of the adult eye. Those that arise from the older tissue are best developed; they are found on the side of the eye. Those closer to the budding zone are minute and indistinct. In *Gomphus* there are only a small number of larger and even-sided facets, the remainder are small and very poorly shaped. In the Libellulines, although the nymphal eye is small, the facets are more regular and most of them are well formed.

The arrangement and distribution of the facets in the adult eye has been much discussed in the previous sections. In Anisoptera the contrasting sizes of the large and small facets first differentiate them abruptly into two main areas occupying upper and lower portions of the eye; then within the area of the small facets those derived from the degenerated nymphal eye, if present, distinguish themselves again from the true adult small facets. As a rule the facets, large or small, bordering the margin of the eye are more or less deformed. When the two eyes are confluent along the top of the head as in the Aeschnines and most Libellulines, the facets along the eye seam are not deformed and in some cases they are even the best formed and are largest of all.

I made a one-by-one count of the number of facets in the eye of a few specimens. I found there are 6,925 facets in the adult eye of *Ischnura verticalis,* 7,274 in the adult eye of *Matrona basilaris,* 8,875 in the adult eye of *Ictinus rapax.* I should say that the accuracy of these numbers is at most 95%, because the facets on the margin, especially those on the lateral border, are indistinct. These numbers, however, covered all the distinct and recognizable facets.

I made four measurements of the size of the facets in the species named in the following tables: 1 and 2. Height and width of eye. 3. Number of large facets per millimeter; the measurement was of the largest facets. 4. Number of small facets per millimeter —the measurement was made on the best formed small facets. The 46 species used represent nearly all the principal groups of the Order.

These records show that in Anisoptera the height (dorso-ventral diameter) of the eye is about twice the width (lateral diameter); the average ratio being 1.93.

In Zygoptera the width of the eye about equals the height, the average ratio being 1.217.

The average ratio of size of large and small facets is in Gomphinae, 2.68; in Aeschnines, 1.69; in Cordulegasterines, 1.66; in Macromines and Cordulines, 1.79; in Libellulines, 2.12; in Zygoptera, 1.31.

In Gomphines the ratio, according to the record, is rather high, due to the fact that in this group the large facets are few and very irregular, and that the measurements of large facets were made to cover only the largest ones.

Within the Libellulines the size of the facets is, to a certain extent, directly proportional to the size of the eye. The small eye has proportionally smaller facets.

MEASUREMENTS OF COMPOUND EYE, AND OF ITS FACETS

Species	Hht of eye	Wth of eye	Ratio	LF N. in 1 mm.	SF N. in 1 mm.	Ratio
Progomphus obscurus	6.5	3.3	1.97	16.0	36	2.25
Ictinus rapax	8.0	5.0	1.60	13.0	29	2.23
Gomphus agricola	4.4	2.8	1.57	11.0	39	3.55
Gomphaeschna furcillata	7.7	3.7	2.08	17.0	28	1.65
Anax parthenope	10.7	5.5	1.95	17.0	28	1.65
Gynacantha subinterrupta	9.83	5.7	1.72	13.5	23	1.77
Cordulegaster dorsalis	9.5	4.8	1.98	19.0	32	1.68
Chlorogomphus infuscatus	11.0	6.0	1.83	15.0	25	1.68
Azuma elegans	12.0	6.3	1.91	13.0	28	2.15
Didymops transversa	6.5	3.3	1.97	21.0	38	1.81
Epicordulia princeps	9.8	5.0	1.96	15.0	25	1.67
Cordulia shurtleffi	7.0	3.5	2.00	21.0	32	1.52
Acisoma panorpoides	4.7	2.5	1.88	22.0	43	1.96
Brachydiplax chalybea	7.6	3.8	2.00	13.5	31	2.38
Brachythemis contaminata	6.4	3.6	1.78	15.5	32	2.13
Brachythemis leucosticta	5.6	3.0	1.86	18.0	38	2.11
Celithemis elisa	6.2	3.2	1.94	15.0	36	2.40
Crocothemis servilia	7.2	3.7	1.94	13.0	38	2.91
Diastatops obscura	4.7	2.6	1.81	28.0	36	1.29
Dielia phaon	7.8	3.9	2.00	16.0	28	1.75
Diplacodes trivialis	5.0	2.7	1.85	17.5	58	2.17
Erythrodiplax minuscula	4.2	2.1	2.00	22.0	44	2.00
Hydrobasileus croceus	9.9	5.1	1.94	14.0	28	2.00
Ladona julia	6.5	3.4	1.91	19.0	35	1.88
Libellula semifasciata	7.5	3.9	1.92	14.0	35	2.50
Leucorrhinia frigida	5.4	3.0	1.80	18.0	38	2.15
Lyriothemis pachygastra	6.6	3.4	1.80	16.0	33	2.06
Neurothemis fulvia	6.8	3.5	1.94	15.0	33	2.20
Orthetrum melania	7.7	3.7	2.08	13.5	29	2.23
Pantala flavescens	8.8	4.3	2.04	16.0	29	1.81
Pseudothemis zonata	8.0	4.0	2.00	15.5	27	1.80
Palpopleura 6-maculata	5.5	2.8	1.96	1.50	36	2.40
Rodothemis rufa	7.3	4.2	1.74	14.0	30	2.14
Rhyothemis fuliginosa	7.1	3.7	1.92	18.0	28	1.56
Ryothemis variegata	7.5	3.7	2.02	17.0	30	1.77
Sympetrum ardens	8.6	4.3	2.00	11.5	29	2.64
Sympetrum corruptum	6.9	3.4	2.03	16.0	32	2.00
Tramea chinensis	9.7	4.7	2.06	13.0	27	2.07
Trithemis festiva	6.8	3.4	2.00	14.0	32	2.08
Pseudophaea opaca	3.8	3.3	1.15	31.0	42	1.36
Taolestes nectans	5.1	4.0	1.27	22.5	31	1.41
Agrion atratum	3.9	3.0	1.30	25.0	34	1.36
Rhinocypha perforata	3.8	2.7	1.41	27.0	37	1.37
Lestes uncatus	3.1	2.7	1.15	38.0	42	1.11
Argia apicalis	2.9	2.5	1.16	38.0	42	1.11
Platycnemis annulata	3.1	2.9	1.07	30.0	38	1.27

Hht of eye = Height of eye
Wth of eye = Width of eye
N. = number

LF = large facets
SF = small facets

LIST OF ABBREVIATIONS

Abmus.Md	Abductor muscle of mandible
Abp.	Abductor apodeme of mandible
Ad.md	Adductor muscle of mandible
Adp.	Adductor muscle of mandible
Ant.	Antenna
At.	Anterior tentorial arm
Br.	Brain
B.Z.	Budding zone
Adm.	Adductor muscle of maxilla
Clp;clp;cly	Clypeus
c.	Anterior articulation of mandible
Cwn.	Crown of hypo-labial frame
DT.	Dorsal tentorial arm
dt.	Dorsal tentorial pit
E.	Compound eye
Epi.S	Epicranial suture
e.	Articulation of maxilla
er.	Epistomal ridge
es.	Epistomal suture
F.C.shf	Fronto-clypeal shelf
Fr.or fr.	Frons
Fr hn.	Frontal horn
g.	Condyle for articulation of the cervical sclerites
Ge.	Gena
Hypo.	Hypopharynx
k.	Trochantin, flexible area between the lower edge of gena and base of mandible
Lat.a	Lateral arm of hypo-labial frame
Lb.or lb.	Labium
LC.	Labial cavity
LF.or lf.	Large facets
LgB.	Longitudinal bands of nymphal eye
Ll.	Lateral lobe of labium
Lm.or lm.	Labrum
LO.	Lateral ocellus
M.	Membrane—2nd cuticle of discarded nym. eye
Md or md	Mandible
Ml.	Median lobe of labium
Mth.	Mouth of hypopharyngeal apodeme
Mx.	Maxilla
Ne.	Nymphal eye
Nt.	New tissue of the growing eye
O.	Median ocellus
Obt.	Orbit
Oc.	Occiput
Oc.F	Occipital foramen
Oc.hn	Occipital horn
Oc.shf	Occipital shelf
Oc.tub	Occipital tubercle
Oc. Tri	Occipital triangle
ocp.	Occipital process
Oes.	Oesophagus
Pol.	Postocular lobe
PoS.	Postocular suture
PT.	Posterior tentorial arm
pt.	Posterior tentorial pit
SF.or sf.	Small facets
Sk.	Shank of hypo-labial frame
Mt.	Mentum of labium
Sm.	Submentum of labium
Smt.pkt.	Small pocket on the base of submentum for the reception of the crown of the hypo-labial frame
t.	Transitional line between the large and small facets
TB.	Transverse dark bands of the nymphal eye peculiar character of the Libellulines
Tk.mus	Trunk muscle bundles
Tnt.	Central body of tentorium
tra.	Tracheal tube
VV.	Ventral triangular projections of the tentorial body
VK.	Ventral hook of the hypo-labial frame peculiar to the Aeschnines
X.	X tissue of the nymphal eye
Vx,or vx.	Vertex
Y.	Y tissue of the nymphal eye — the pigmented functional nymphal eye
Ya.	The new tissue of the Y tissue of the last instar; is destined to form the true small ommatidia of the adult eye
Z.	Z tissue of the nymphal eye peculiar to the Libelluline nymphs; is destined to form the small ommatidia of the adult eye

Plate VII

Illustrations of the Principal Types of Odonate Head

(Front aspects)

Fig. 1. *Gomphus agricola*
2. *Chlorogomphus infuscatus*
3. *Pantala flavescens*
4. *Diastatops obscura*
5. *Anax junius*
6. *Epiophlebia superstes*
7. *Agrion atratum*
8. *Lestes forcipatus*
9. *Platycnemis annulata*

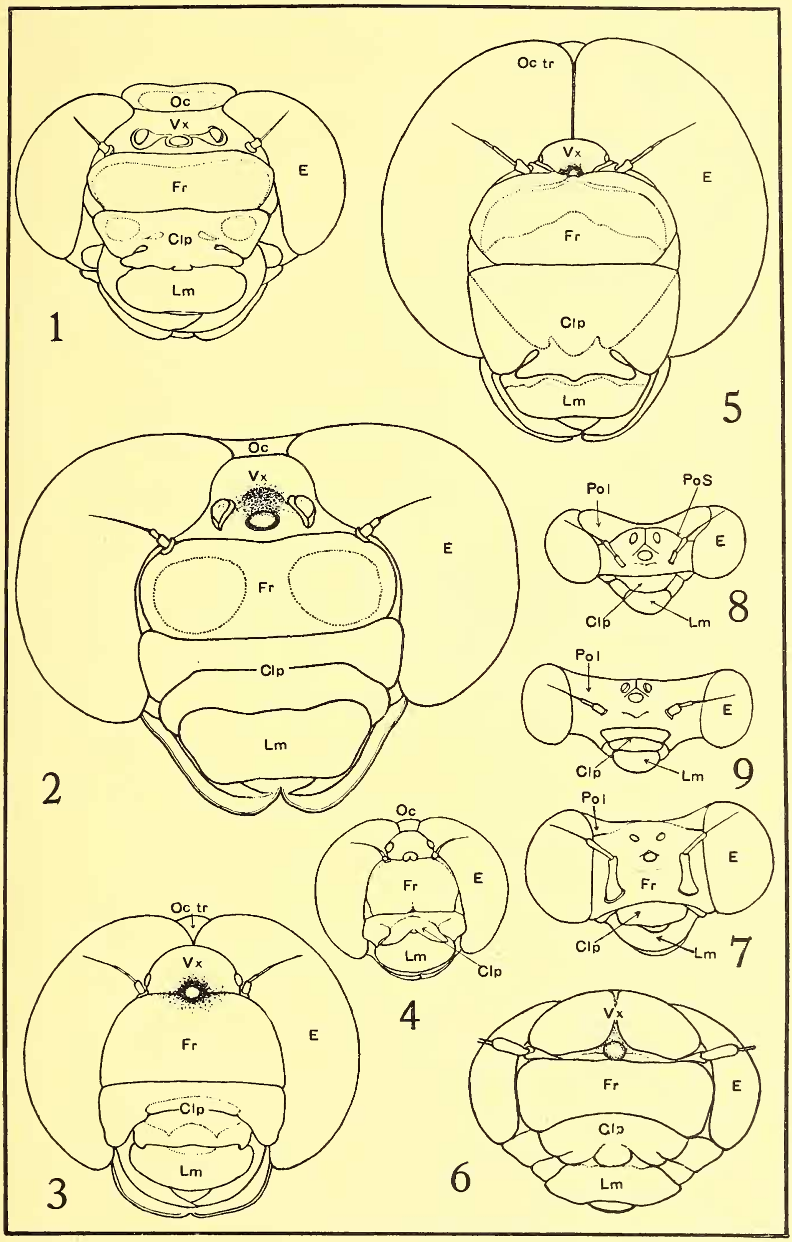
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Plate VIII

Illustrations of the Principal Types of Odonate Head

(Dorsal views)

Fig. 1. *Gomphus agricola*
2. *Chlorogomphus infuscatus*
3. *Pantala flavescens*
4. *Diastatops obscura*
5. *Anax parthenope*
6. *Epiophlebia superstes*
7. *Agrion atratum*
8. *Coenagrion barbatum*
9. *Gomphus flavicornis* ♀

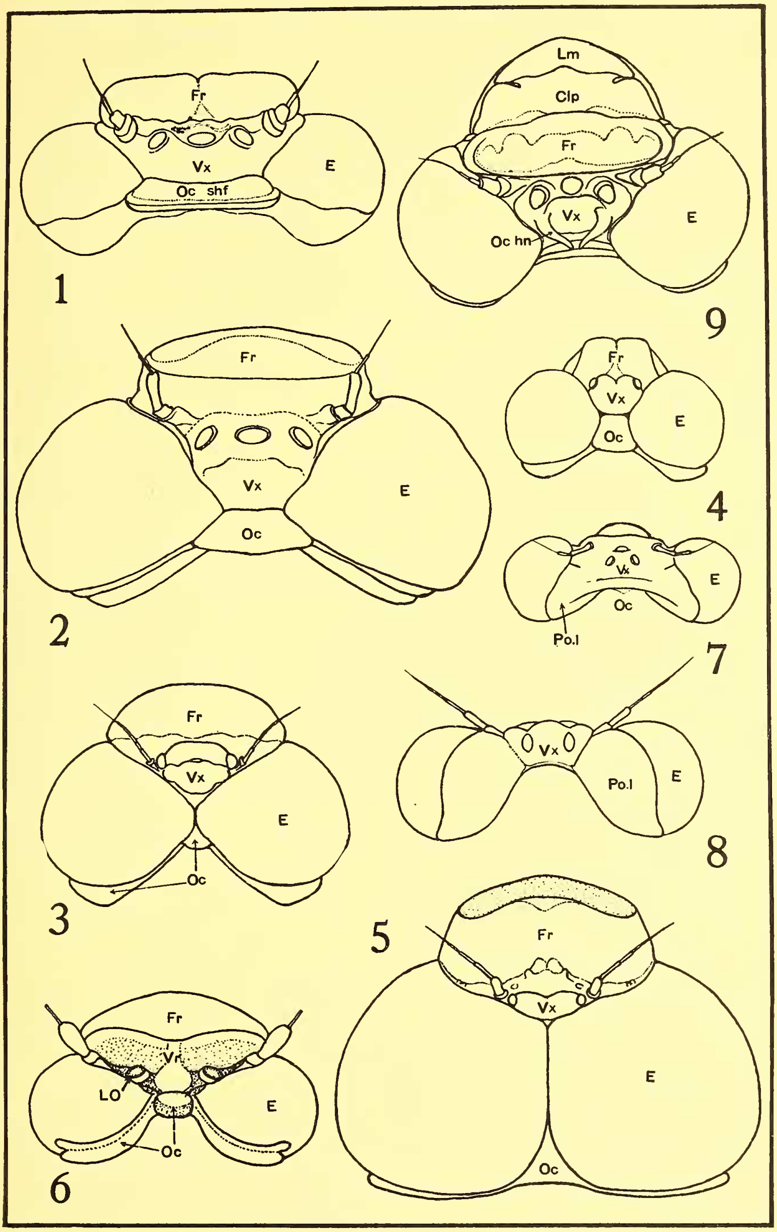
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Plate IX

Illustrations of the Endoskeleton of the Nymphal Head

Fig. 1. Dorsal aspect of nymphal head of *Anax parthenope*, showing the external tentorial elevation (DT).

2. Nymphal head of *Gynacantha subinterrupta*, showing the ventral aspects of the tentorium.

3. Nymphal head of *Gomphus agricola*, showing ventral aspects of the tentorium and the hypo-labial frame.

4. Nymphal head of *Gomphus agricola*, showing dorsal aspects of the tentorium.

5. Hypo-labial frame of *Gynacantha subinterrupta*, showing ventral aspects of the structure.

6. Lateral view of the hypo-labial frame of *Gynacantha subinterrupta*, showing the ventral hook (VK).

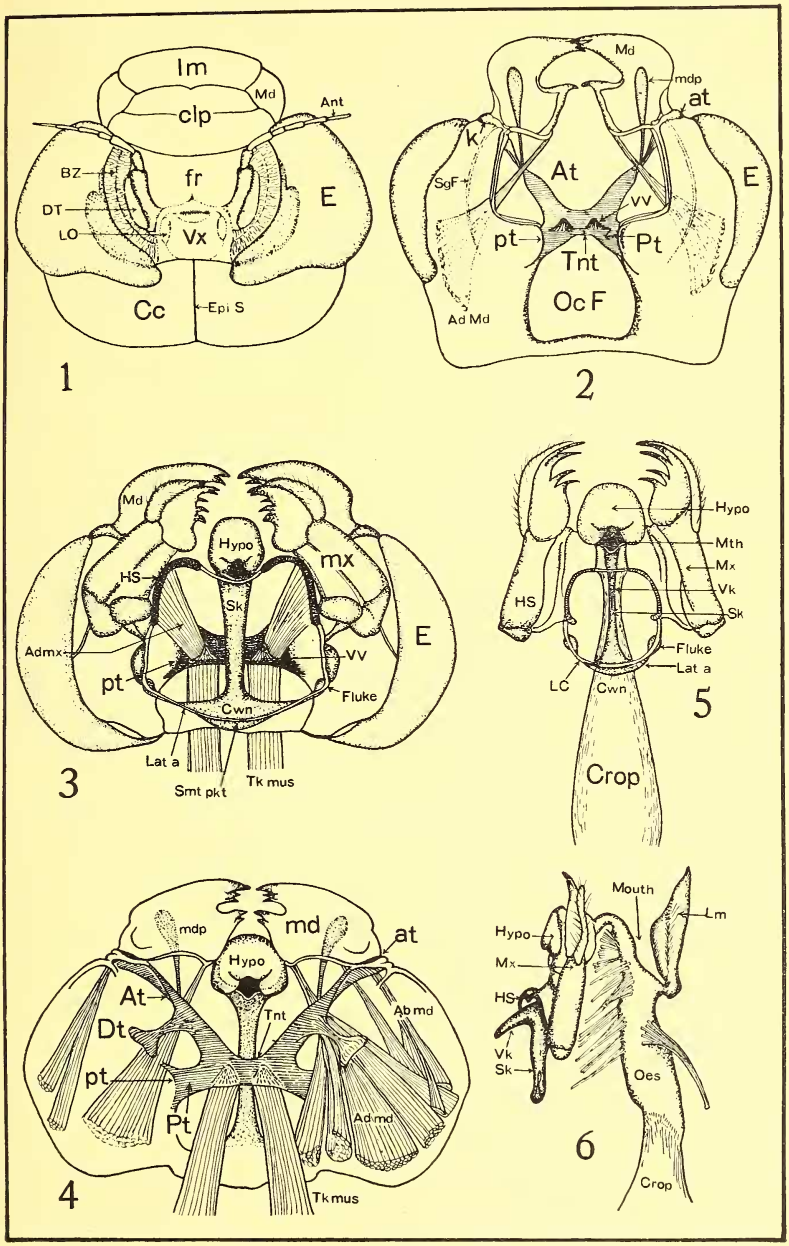
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Plate X

Illustrations of the Endoskeleton of the Adult Head

Fig. 1. Head of *Anax parthenope,* lateral view, showing construction of the orbit.

2. Head of *Pantala flavescens,* showing relative positions of the tentorium (left) and facial sclerites (right).

3. Caudal aspects of head of *Tramea chinensis,* showing the occipital process (Ocp).

4. Head of *Anax parthenope,* showing lateral aspect of the tentorium of the Aeschninae.

5. Head of *Gomphus agricola,* showing front aspect of the tentorium of a Gomphine.

6. Head of *Gomphus agricola*, showing caudal aspect of the tentorium.

7. Head of *Gomphus agricola* sectioned at the mesal line, showing construction of the tentorium, and especially the tentorial body.

8. Lateral view of tentorium, head of *Gomphus agricola* with the compound eye removed.

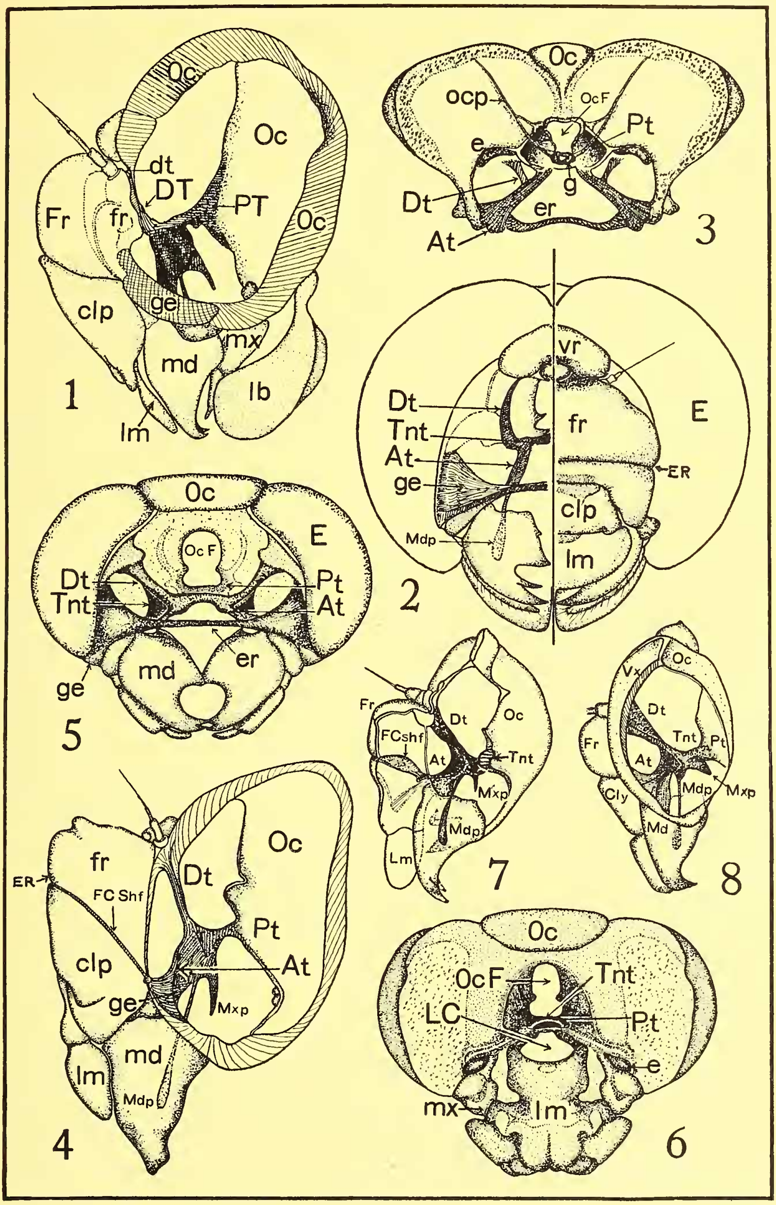
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Plate XI

The Various Forms of the Antennae of Odonata

I. *Antennae of the Nymphs:*

A. Petalura
B. Hagenius
C. Gomphus
D. Aeschna
E. Platycnemis
F. Rhinocypha
G. Libellula
H. Agrion

II. *Antennae of the Adult:*

1. Gomphus
2. Chlorogomphus
3. Anaciaeschna
4. Tetragonuria
5. Hydrobasileus
6. Nannophya (highly magnified)

6a. Nannophya

7. Anotogaster
8. Gomphaeschna
9. Epophthalmia
10. Caliaeschna
11. Zonophora
12. Taolestes
13. Lestes
14. Coenagrion
15. Platycnemis
16. Pseudophaea
17. Hetaerina
18. Agrion
19. Agrion
20. Rhinocypha

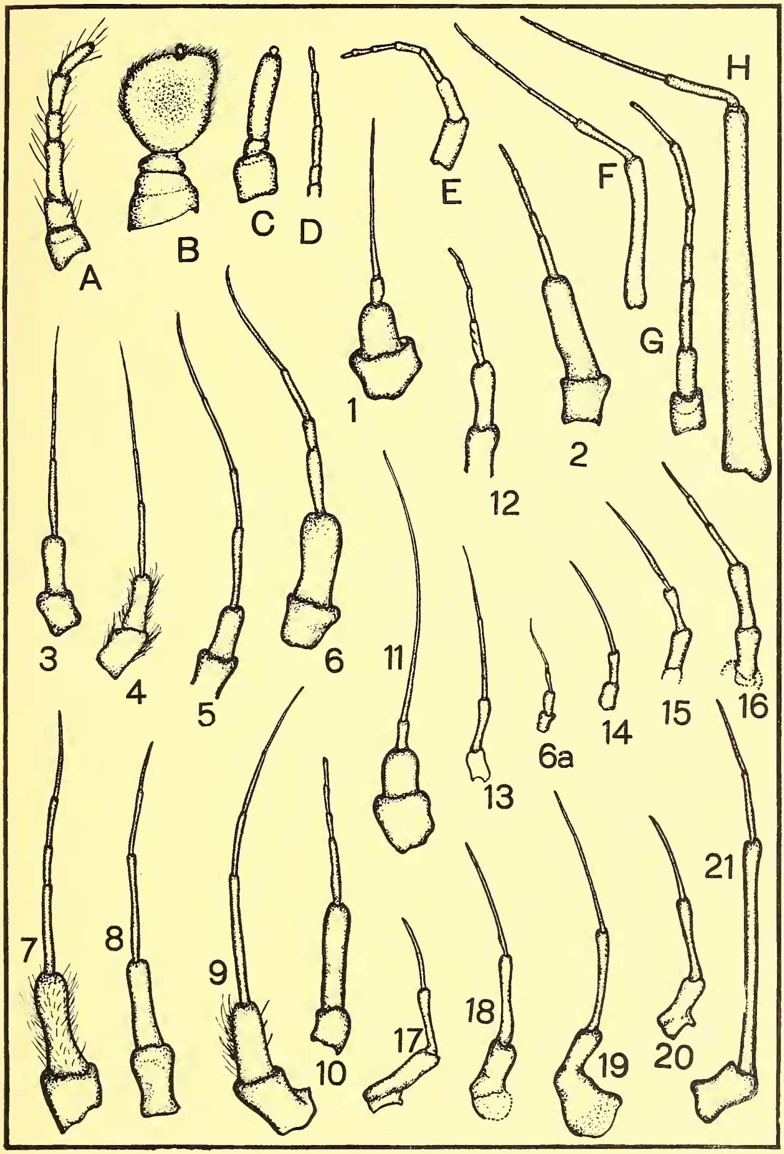
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Plate XII

Record of Experiment on the Development of the Nymphal Eye in Five Successive Instars of Aeschna umbrosa

Figs. 1–4. Drawn from exuviae.
Fig. 5. Drawn from nymphal head.

Small numerals, 1, 2, 3, 4, 5, mark positions of punctures and scars.

X designates the tissue that is destined to form large ommatidia of the adult eye.

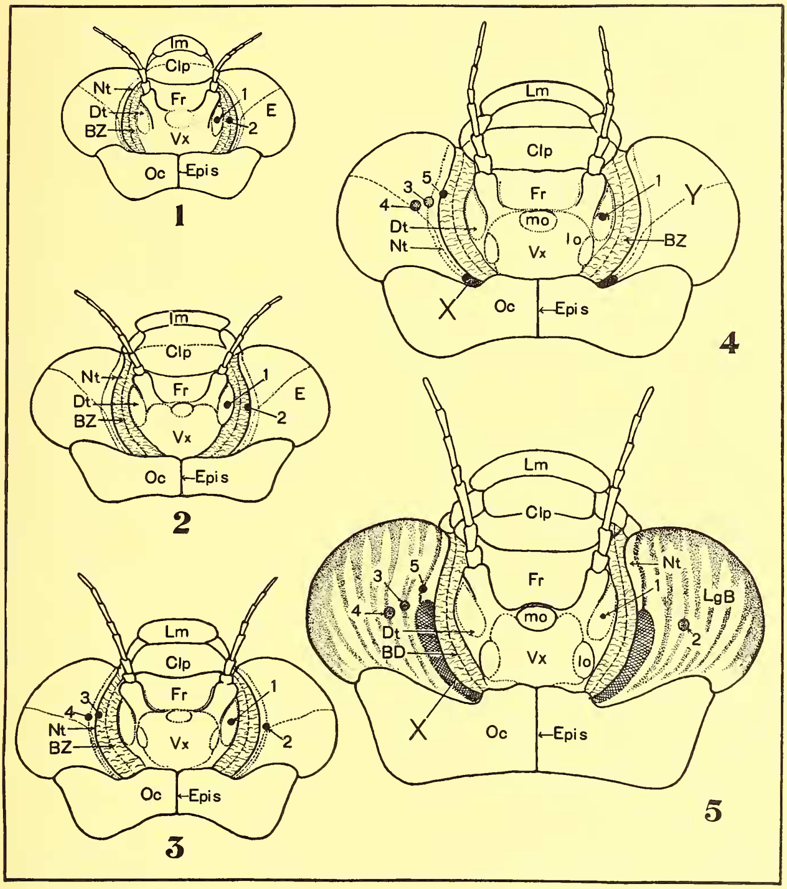

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PLATE XIII

Experiments on the Development of the Compound Eye During Metamorphosis

(*Aeschna umbrosa*)

Fig. 1. Small numerals 1 to 21 record positions of punctures made on nymphal head.

Figs. 2 to 4. Record by the same numbers the positions of the scars of the wounds as they appear on the adult's head.

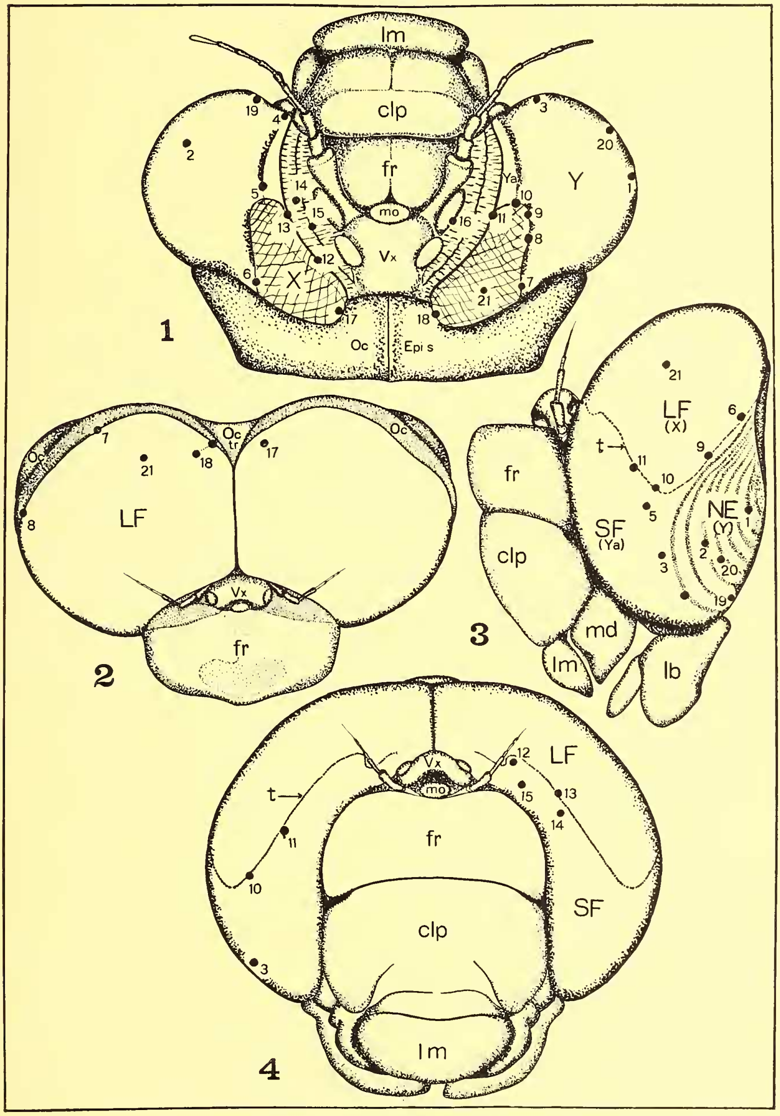
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Plate XIV

Illustrations of the Principal Types of the Nymphal Head of Anisoptera

(Lateral aspects)

Fig. 1. Pantala
2. Petalura
3. Gynacantha
4. Gomphus
5. Epophthalmia
6. Aeschnophlebia
7. Cordulegaster

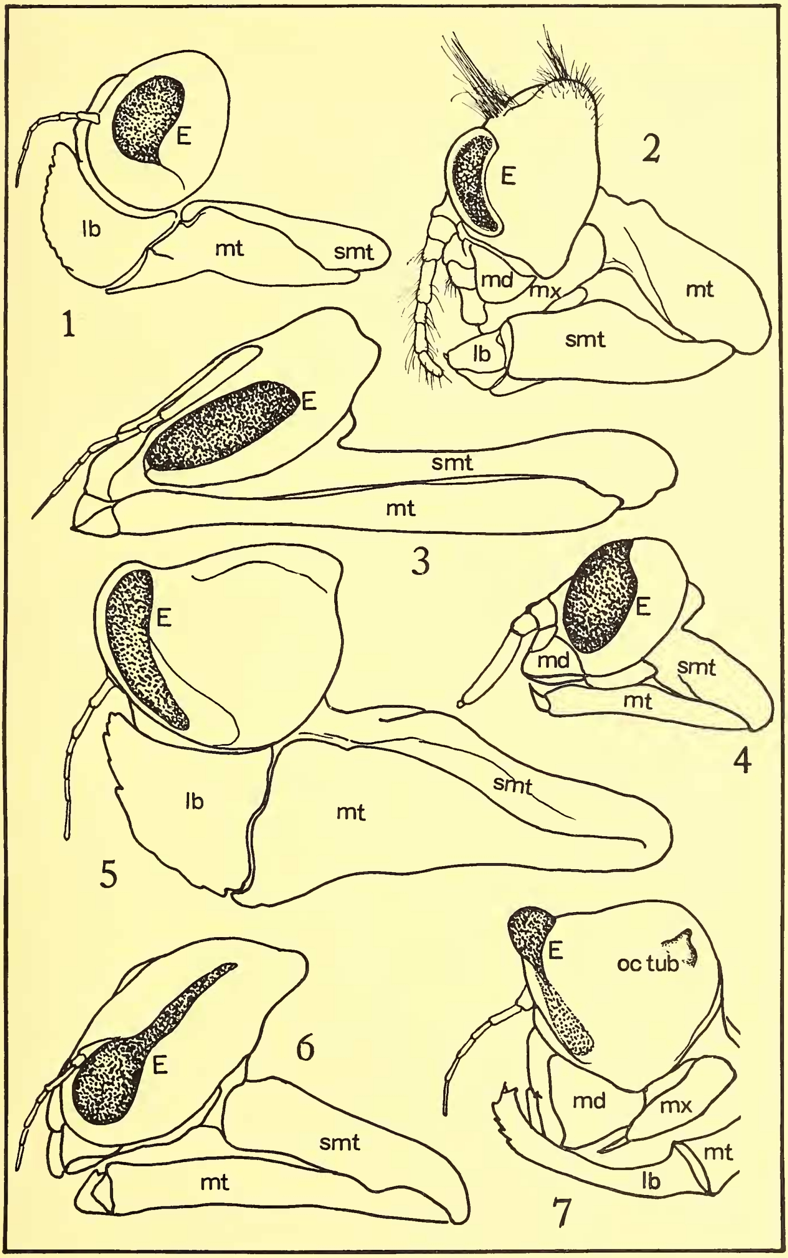
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Plate XV

Experiments on the Development of the Compound Eye During Metamorphosis

I. *Record of Experiment on Anax junius:*

Figs. 1, 2, 3. The exuviae of the last three instars, showing development of the X tissue.

3. Also records the positions of the punctures made on the nymphal head.

4. Adult head records positions of scars of wounds after metamorphosis.

II. *Record of Experiment on Gomphus lividus:*

Fig. 5. Adult head of *Gomphus lividus* records positions of scars of wounds after metamorphosis.

6, 7. Nymphal head, showing positions of punctures.

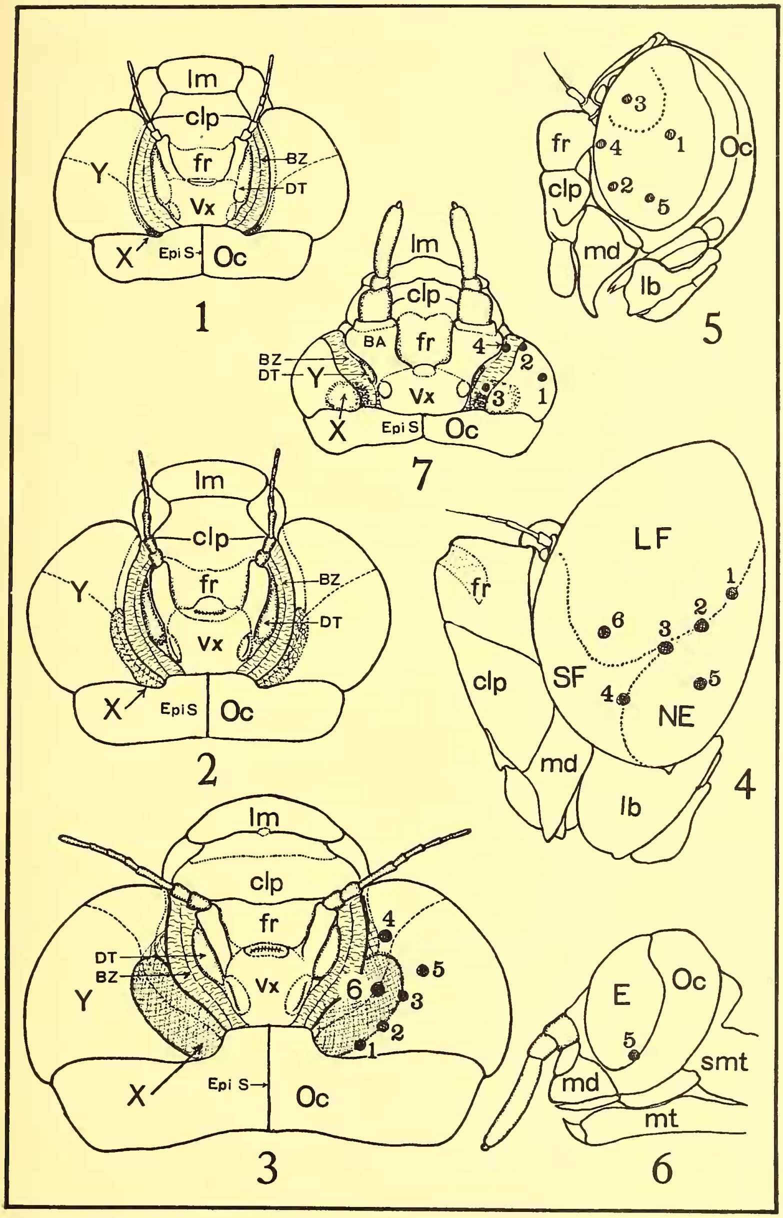
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Plate XVI

Experiments on the Development of the Compound Eye During Metamorphosis

I. *Record of Experiments on Tetragonuria cynosura:*

Fig. 1. Nymphal head, showing positions of punctures.
2. Lateral aspect of adult head, showing positions of scars of wounds. The Y tissue is pushed to the side, making a jog on the lateral margin.
3. Same, dorsal view.

II. *Record of Experiments on Libellula pulchella:*

Fig. 4. Nymphal head, showing positions of punctures.
5. Dorsal view of adult head, showing positions of scars of the wounds.
6. Lateral aspect of adult head, showing the same. No. 17, made on the tentorial elevation of nymphal head, is not recovered.

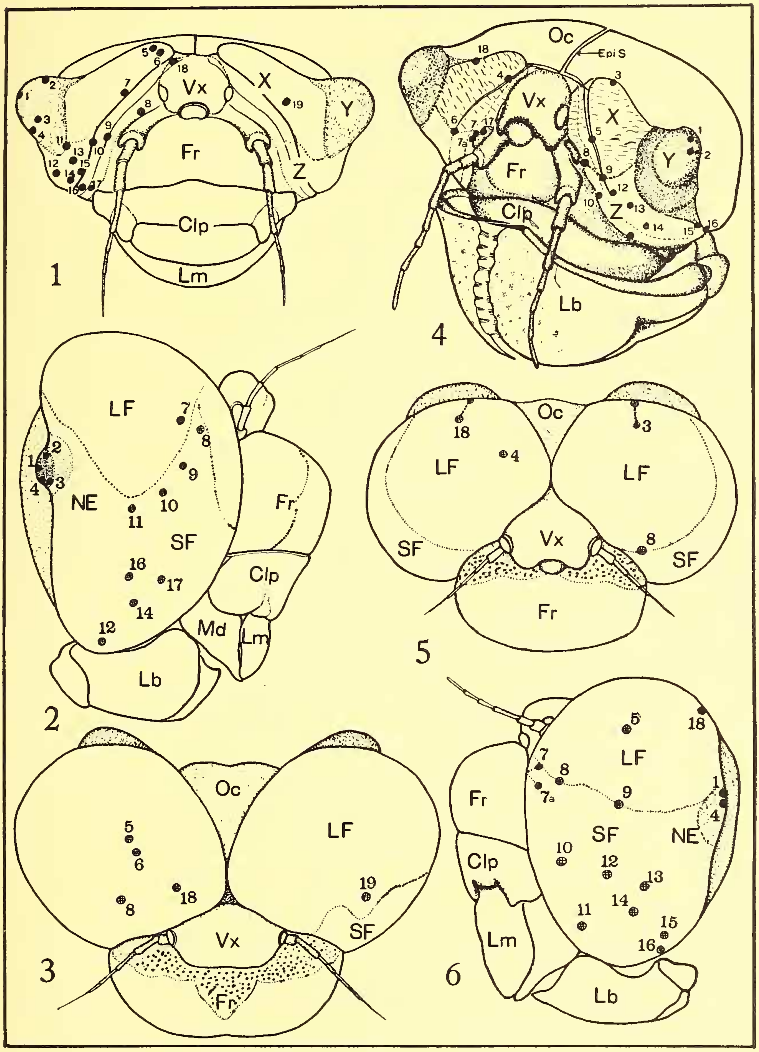
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Plate XVII

Illustrations Showing the Fate of Nymphal Eyes after Metamorphosis in the Different Groups of Libellulidae

Figs. 1 & 1a. Front and dorsal aspects of nymphal head of *Didymops transversa.*
1b. Lateral aspect of adult eye.
Figs. 2 & 2a. Front and dorsal aspects of nymphal head of *Tetragonuria cynosura.*
2b. Lateral aspect of the adult eye.
Figs. 3 & 3a. Front and dorsal aspects of nymphal head of *Plathemis lydia.*
3b. Lateral aspect of the adult eye.
Figs. 4 & 4a. Front and dorsal aspects of nymphal head of *Libellula pulchella.*
4b. Lateral aspect of the adult eye.

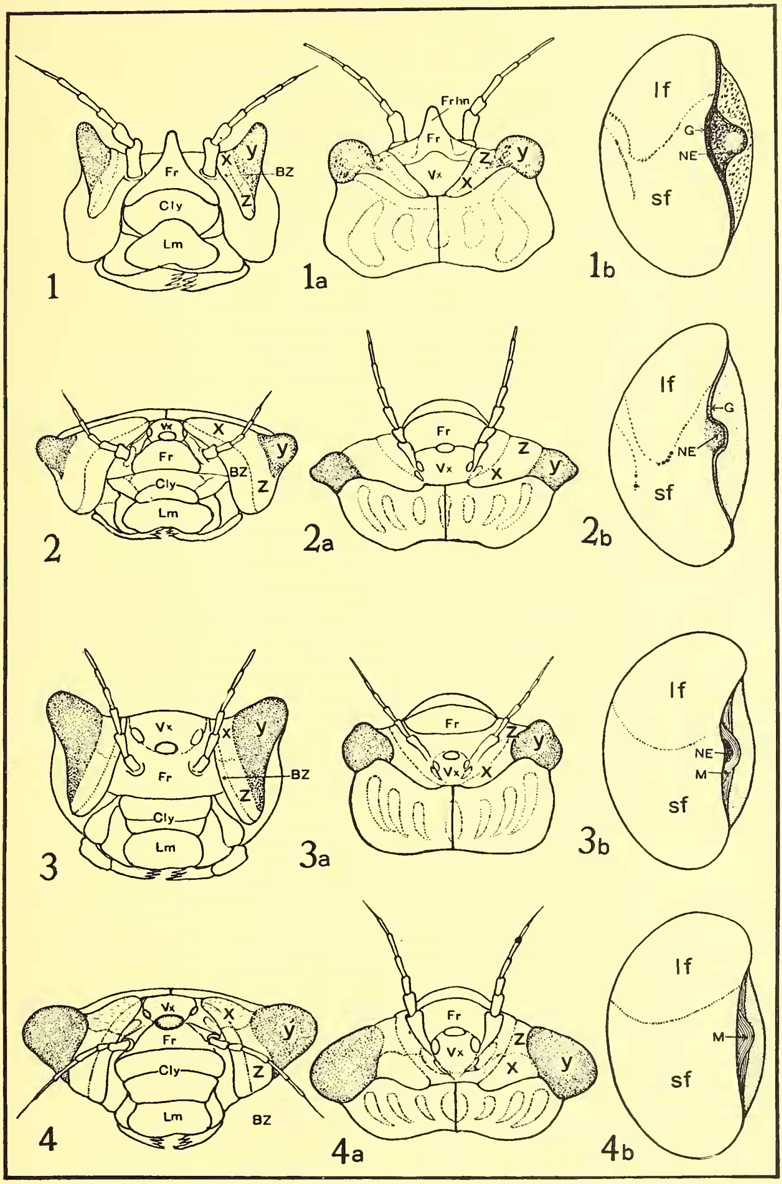
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Plate XVIII

Features of the Mature Nymphal Head of Libellulines

Fig. 1. A cross section of mature nymphal head of *Sympetrum vicinum,* showing X and Y tissues and the post-retinal layer.
Fig. 2. Fully mature nymphal head of *Mesothemis,* showing the expansion of the X tissue (X, X, X) shortly before metamorphosis.
Fig. 3. Head of mature nymph of *Plathemis lydia,* showing the longitudinal pigment bands, the transverse bands and the X, Y, Z tissues.
Fig. 4. Head of mature nymph of *Sympetrum vicinum,* showing transverse bands (TB) and X, Y, Z tissues.
Fig. 5, 6. Nymphal head of *Sympetrum vicinum,* showing tracheation and pigments of the surface of the brain.
Fig. 7. Dorsal view of the same.
Fig. 8. Exuvium of Libelluline, showing the cleft of the molting on the thorax and head, particularly of the eye region.